

A REVISION OF NORTH AMERICAN POTAMOGETON SUBSECTION PUSILLI (POTAMOGETONACEAE)¹

ROBERT R. HAYNES

The importance of the aquatic environment is becoming more evident with our present ecological concerns. Many aquatic plants have been shown to be indicators of water quality and of changes in the aquatic environment (Volker & Smith, 1965; Lind & Cottam, 1969; Harman & Doane, 1970; Stuckey, 1971; Wentz & Stuckey, 1971). Certain species, e.g. *Najas minor*, *Potamogeton foliosus*, *P. pusillus*, and *Vallisneria americana*, are tolerant of polluted waters. Other species, e.g. *Najas flexilis*, *Potamogeton amplifolius*, *P. friesii*, and *P. strictifolius* are intolerant.

Early workers, e.g. Pond (1905) and Shelford (1918, 1937), considered aquatic vascular plants of little value in the food chain of aquatic animals. Later workers, e.g. Moore (1915), Moyle and Hotchkiss (1945), and Welch (1935, 1952), however, considered the aquatic vascular plants an important source of food for aquatic animals. In a survey of literature on the significance of aquatic vascular plants in the nutrition of animals, Gaevskaya (1966) considered the aquatic vascular plants as a primary source of food for animals of the aquatic environment.

According to Martin (1951), the pondweeds (*Potamogeton*) are probably more valuable to ducks than any other group of plants in the United States. Trautman (1957) indicates that the distribution in Ohio of certain species of fish is contingent upon that of associated pondweeds. Gaevskaya (1966) lists 124 species of animals (89 invertebrates and 35 vertebrates) that feed upon *Potamogeton*.

¹Contribution from the Botany Department, The Ohio State University (Paper No. 867). Portion of a Ph.D. dissertation written at The Ohio State University. Field work for two summers was supported by The University of Michigan Biological Station and for one summer in part by a Research Grant from the Ohio Academy of Science and Sigma Xi Grant-in-Aid for Research.

The plants also serve as shelter for panfish and young fish of other species. Many aquatic insects have at least one stage of their life cycle, if not their entire life cycle, upon the vegetative structures of the pondweeds (Welch, 1952). These insects are, in turn, preyed upon by fish and some birds. Müller-Liebenau (1956) found 294 invertebrates in beds of five species of *Potamogeton* in the lakes of eastern Holstein. The pondweeds are, therefore, a major factor in the food cycle of the aquatic environment. In fact, among the submerged and floating-leaved species of aquatic vascular plants, Gaetskaya (1966) states that as regards distribution, productivity, and trophic relations of aquatic animals, *Potamogeton* is the most important genus.

Potamogeton Linnaeus is a cosmopolitan genus with approximately 100 species of submerged and floating-leaved aquatic plants. The genus has been separated into two subgenera (Raunkiaer, 1896) and numerous sections and subsections (Graebner, 1907; Hagstrom, 1916). The North American representatives of one of the latter, *Potamogeton* subsection *Pusilli* Graebner (narrow-leaved pondweeds), are the subject of this paper. The *Pusilli* can be separated from the other taxa of the genus by their 3-7(-9)-nerved leaves that are 2-5 mm broad, by their stipules free from the blade, and by their small (to 4.0 mm long) fruits that normally are produced terminally.

Although the *Pusilli* have been included in at least four revisionary treatments (Morong, 1893; Ascherson, 1907; Hagstrom, 1916; Fernald, 1932), uncertainty still exists as to the number of taxa to be included in the group and at which rank these taxa should be recognized. Taylor (1909), for example, accepted only six taxa; Ogden (1957) divided the group into 18 taxa; Muenscher (1944) recognized only 12 taxa; Fernald (1932) acknowledged 21 taxa.

The *Pusilli* have been considered difficult taxonomically for many years (Fassett, 1940) and, in fact, many of the recently collected specimens from North America have been extremely difficult, if not impossible, to identify. The reasons for these difficulties may have been: 1) the *Pusilli*

are morphologically small and, thus, the characters are difficult to observe; 2) vegetatively (the condition in which much of the material is encountered) the species superficially resemble each other; 3) ecological variability has not been fully understood; 4) the nomenclature has been confused. Many authors in the past have not recognized the vegetative variability of the species. As a result, more than 60 names have been proposed for the taxa of North American *Pusilli*.

Because of the apparent economic importance of the group, it is essential to understand the taxonomic relationships within the genus. As stated above, this understanding has not previously been accomplished. Therefore, I considered that the subsection *Pusilli* was in need of a thorough revision. It is understood that problems still exist within the *Pusilli*, but it is hoped this re-evaluation will clarify some of the confusion within the group.

TAXONOMIC HISTORY

Potamogeton was first described by Tournefort (1719) who recognized 13 species. Linnaeus (1753), basing his treatment upon that of Tournefort, accepted 12 species. Since that time, a proliferation of names has occurred, both at the generic and infra-generic levels, resulting in considerable chaos of the nomenclature. However, because of the nomenclatural confusion and the fact that I am treating only the *Pusilli*, a brief outline of the major events is presented rather than a detailed discussion of the history.

- 1788. Walter applied *Potamogeton* to two species of *Myriophyllum* (Haloragaceae).
- 1790. Loureiro named *Hydrogeton*, based on *P. heterophyllum*.
- 1819. *Peltopsis* was created by Rafinesque, based on *Potamogeton perfoliatus*.
- 1837. Koch divided the genus into five sections: *Chloephylli*, *Coleophylli*, *Enantiophylli*, *Heterophylla*, *Homophylla*.

1845. Reichenbach recognized five major groups, without giving these groups formal rank: *Antiphyllogeton*, *Chloegeton*, *Coleogeton*, *Heterophyllogeton*, *Homophyllogeton*.
1845. *Spirillus* was named by Gay, without any species having been listed.
1858. Irmish divided the *Homophylla* of Koch into two sections, naming the new one *Batrachoseris*.
1896. Raunkiaer placed all Danish species into two subgenera: *Coleogeton* and *Eupotamogeton*.
1903. Raunkiaer divided the genus into 16 groups, which were not given any formal taxonomic rank.
1907. Graebner (in Ascherson & Graebner) gave formal rank to most of Raunkiaer's groups (mostly at the subsectional level) and named several other subsections.
1913. Nieuwland transferred 20 species of *Potamogeton* to *Spirillus*.
1916. Hagstrom named several new sections and numerous subsections.

Potamogeton subsection *Pusilli* was first recognized as a natural unit by Raunkiaer (1903). He gave no formal name to the group, but referred to it as "*P. pusillus*-group." Graebner in Ascherson and Graebner (1907) combined two of Raunkiaer's groups — *P. pusillus*-group and *P. confervoides*-group — into the subsection *Pusilli*. Based upon characters of the stem anatomy, Hagstrom (1916) removed *P. confervoides* from the subsection. Hagstrom's concept of the group was the one followed by Fernald (1932; 1950) and accepted in the present work.

MORPHOLOGY

HABIT: The *Pusilli* are rooted linear-leaved obligate aquatic plants that grow totally submerged except for the spikes, which are usually extended above the surface of the water. When fruiting, the spikes are normally withdrawn below the surface so that the plant is again totally sub-

merged. The mature plants, at least in the temperate regions, are mostly functionally annuals, which overwinter as seeds, winter buds, or turions. The winter buds are produced in such abundance that Fernald (1932) and Hagstrom (1916) were of the opinion that the plants rarely reproduced by seeds, but instead reproduced by winter buds. These conclusions were based upon a high percentage of plants having been collected with the winter buds still attached. Muenscher (1938), however, has shown that for *Potamogeton pusillus* [var. *tenuissimus*], at least, and possibly for other *Pusilli*, the young seedlings are very similar to a winter bud and these could easily be mistaken for old winter buds.

STEM: The stems of the *Pusilli* are erect to decumbent or prostrate, depending upon the water depth and rate of water flow, and are round to compressed in cross section. Ogden (1972) has suggested that no species of the *Pusilli* from New York possess a rhizome. This statement implies that the stem arises from a winter bud or a similar structure formed from the seedling as illustrated by Muenscher (1936). This situation probably represents the majority of the cases. However, some taxa, such as *Potamogeton hillii*, may produce a rhizome if the stem becomes decumbent and subsequently becomes covered by debris. Rooting at the nodes may then occur, and a rhizome-like structure several centimeters in length would be formed. Ogden (1966), in fact, illustrated a rhizome of *P. foliosus* from Texas.

Slight variation in the shape of the stem in cross-section and in the number and sizes of ridges along the stem has been observed. Certain species, e.g. *Potamogeton foliosus* and *P. friesii*, may have compressed stems, whereas other species, e.g. *P. pusillus* and *P. clystocarpus*, usually have terete stems. However, at certain times the stem of all species may be slightly compressed. Therefore, stem characters used for identification are helpful only as supplemental evidence.

Raunkiaer (1903), Hagstrom (1916), and Ogden (1943) have utilized stem anatomy for distinguishing certain species of other sections of *Potamogeton*. However, the stem anatomy of the various species of the *Pusilli* is so similar that this character is of little or no use to separate the species.

At the nodes of some species, a pair of translucent oil glands may be present; in other species, they are extremely uncommon. The glands range in color from white, cream, gold, brown, or green, and in diameter from 0.1-1.0 mm. When present, by variations in color and size, the glands can be useful supplemental evidence. As with the lacunae, their presence (or absence) should not be relied upon absolutely, as they are apparently a physiological response to unknown ecological factors.

LEAF BLADES: The blades of the *Pusilli* are rufescent, green, pellucid, to nearly black, setaceous to linear, non-lunate, sessile, stipulate, and acute to obtuse or apiculate. Venation is parallel with 1-9 veins (nerves). The lateral nerves join the midrib at or just below the apex. In some species, one to several rows of lacunae parallel the midrib. To my knowledge, no one has studied the development or structure of the lacunae of *Potamogeton*. Singh (1964) studied the vegetative structures of various species of Potamogetonaceae, including *P. berchtoldii* [*P. pusillus* var. *tenuissimus*], which is characterized by having lacunae bordering the midrib. If Singh noticed any lacunae, he made no mention of them. Fernald (1932) suggested they are rows of nearly empty and colorless cells, presumably giving buoyance to the leaves. To my knowledge, the origin and functions of the lacunae are not known. However, regardless of their origin, the lacunae appear as light lines on each side of the midrib. The individual rows can be observed with 10× magnification, which would indicate that each row is several cells in width, rather than one cell wide. The lacunae are useful for identification, as some taxa rarely possess them, whereas others commonly have 1-

several rows on each side of the midrib. This character usually serves as good supplemental evidence when used in conjunction with other features, preferably reproductive ones.

Recognition of many taxa of *Potamogeton*, especially of the *Pusilli*, has been based upon slight morphological differences in the leaves (Hagstrom, 1916; Fernald, 1932). Dandy and Taylor (1940) suggested that, due to different ecological conditions, the vegetative variability of the species is too great to be useful as the only criterion for naming a new taxon. During the present study I have observed that several populations undergo a seasonal dimorphism, e.g., producing two morphologically dissimilar sets of leaves in one growing season. Often, plants of *Potamogeton pusillus* var. *tenuissimus* produce in the early summer a set of obtuse leaves that are near the limits of width for the species and which possess four to five rows of lacunae on each side of the midrib. Later in the growing season, these leaves die and a new set is formed. The leaves of this second set are usually acute, quite narrow, and possess only one to three rows of lacunae. If one were to follow Fernald's (1932) taxonomy of this group, one could correctly identify the plant as one variety in the early summer and another variety in the fall. The cause of this seasonal variation is unknown. Since the same genotype may produce two sets of leaves, each morphologically distinct, these vegetative characters should be considered with caution when attempting to distinguish taxa.

STIPULE: Associated with each leaf blade and surrounding the stem of the *Pusilli* is a tubular or convolute stipule. The stipules are free from the leaf blades and vary in color from white to brown to green. The number and coarseness of the veins varies from one species group to another. This vein character, along with the stipule color, can be useful for identification of species. In some taxa, e.g. *Potamogeton friesii*, the stipules are white with many coarse veins. With age the interveinal tissue near the apex decays leaving the coarse veins extending as fibers past the

remaining interveinal tissue. In other species, e.g. *P. pusillus*, the stipules are usually brown to green with only a few veins, these being quite delicate. With age, the vein tissue decays along with the interveinal tissue.

Hagstrom (1916) considered the tubular versus convolute condition of the stipules to be of great evolutionary significance. He, in fact, divided the *Pusilli* into two series — *Pusilli Convoluti* and *Pusilli Connati* — based on no characters other than the connation of the stipules. Later workers, Dandy and Taylor (1938), Ogden (1966), and Voss (1972) have accepted this character as important for determining species but have not accepted its use in separating the subsection into two series. For one of the species complexes in which the stipule character is considered most useful, according to Hagstrom and Fernald, — that being *P. pusillus* and *P. panormitanus* [*P. pusillus* var. *tenuissimus* and var. *pusillus*, respectively], I have compared the character with other vegetative and reproductive characters considered important by these workers. The data obtained from this comparison indicate only about a 70-80% correlation of this character with the other characters. In my opinion, when the situation is either the presence or absence of a character, for that character to be given such high value in a classification system, there should be little variability of that character within a taxon.

WINTER BUDS: The winter buds (turions) are vegetative reproductive structures that function as agents for multiplication of the individuals and as perennating organs during the unfavorable season. Yeo (1966) planted one winter bud of *Potamogeton crispus* on 1 Apr. 1963. At the end of the growing season, 23,520 winter buds had been produced. This is obviously a very effective method of propagule production. In some species, the winter buds are produced early in the growing season and may, therefore, germinate to produce new plants that year. In other species they are produced only at the end of the season, and do not germinate until the following year.

The winter buds consist of a short stem apex with shortened internodes. The leaves of the structures can be divided into two types: outer and inner. The outer leaves usually resemble the vegetative leaves, but the inner leaves may not. The inner leaves may be numerous, shortened, and oriented in a plane perpendicular to that of the outer leaves, thus giving a fan-shaped appearance, as in *P. friesii*. On the other hand, the winter buds may be few to several, compacted, and rolled into a hardened structure, thus appearing fusiform, as in *P. pusillus*. Finally, they may be various in number and similar to the vegetative leaves, as in *P. obtusifolius*.

As indicated above the winter buds may be useful as characters for the identification of the *Pusilli*. Hagstrom (1916) and Fernald (1932) have placed emphasis upon the location on the plant of the structures. I consider the location of the structure too variable to be of taxonomic value. Instead, the size of the structure and the modification of the inner leaves are of significant taxonomic value.

INFLORESCENCE: The inflorescence of the *Pusilli* is either a capitate or cylindric spike consisting of from one to five whorls of four flowers each. Some authors have considered this structure to consist of a reduced compound spike (see comments under discussion of the flower). The inflorescence is a very good character for distinguishing species of the *Pusilli*. Important features are the length, shape, and number and separation of the whorls of the inflorescence. In some taxa, e.g. *Potamogeton pusillus* var. *pusillus*, with an inflorescence of more than three whorls, the whorls will usually be separated; however, in other taxa, e.g. *P. foliosus*, the whorls are rarely separated.

PEDUNCLES: The peduncles of the *Pusilli* are either terminal on the stem or axillary to vegetative leaves. Often, axillary peduncles are reflexed, whereas the terminal ones usually are erect. In longitudinal section, the peduncles either have parallel sides or are clavate. In cross sections,

they range from nearly terete to so compressed that they are three to four times as broad as high.

The peduncle is often a very good character for distinguishing taxa of the narrow-leaved pondweeds. In *Potamogeton foliosus* for example, the peduncle is short, clavate, usually reflexed, and axillary. In *P. pusillus* var. *pusillus*, on the other hand, the peduncle is elongate, parallel-sided, erect, and usually terminal.

FLOWER: The flowering structures of *Potamogeton* have been interpreted variously. First, Eames (1961) interpreted each perianth segment as a sepaloid bract subtending and adnate to the corresponding stamen. He, therefore, regarded the flower of *Potamogeton* as an inflorescence comprising four staminate flowers, each of a single stamen and its adnate bract, and four apetalous carpellate flowers, each of a single carpel with one campylotropus ovule. By this interpretation, the spike represents a reduced compound inflorescence. Second, based upon vascular anatomy and floral morphology of seven species of *Potamogeton*, Singh (1965) chose to consider the flower of *Potamogeton* as a normal flower with four perianth segments. Finally, Sattler (1965) considered it impossible to classify the structure as a true flower or as an inflorescence, because it displayed characters of both. He questioned the classical use of flower and inflorescence as two separate categories and emphasized the need for more developmental work in the "Helobiales" (an order that is now considered to be the Alismatidae). For the sake of convenience, Singh's concepts are followed in this revision.

Controversy has also existed as to the real nature of the perianth-like structures that are adnate to the stamens. Ascherson (1889) and Rendle (1930) considered the structures to be outgrowths of the stamens. They then called the structures stamen connectives. Sattler (1965) and Singh (1965) have reached a different conclusion. Sattler, for example, demonstrated in *Potamogeton richardsonii* that these structures are initiated on the floral apex prior

to stamen initiation. Thus, they cannot be outgrowths of the stamens. He instead considered them to be perianth segments. After inception of the stamen primordia, growth occurs between the perianth primordia and that of the stamen. Thereby, the base of the developing stamen and perianth become united. The perianth is usually light green to greenish brown in color and consists of two parts — a claw and an expanded upper portion — each of approximately equal length.

The gynoecium consists of four separate, superior, uniovulate carpels with parietal placentation. The androecium consists of four bithecate stamens. Anthesis usually is approximately at the time of embryo sac maturity (Lawrence, 1951).

Among the various taxa of the *Pusilli*, only slight morphological variation exists in the flowers. These structures, therefore, are of little value for distinguishing species. However, the size of the structures often is quite useful for separating various subsections of the genus.

FRUITS: The fruits of the pondweeds have been variously classified — e.g., as a drupe (Reichenbach, 1845), as a drupelet or drupaceous (Morong, 1893; Fryer and Bennett, 1915), as a drupe or an achene (Clapham et al., 1962) and as a druplet or nutlet (Lawrence, 1951). The use of such an array of terms suggests that no one term could adequately describe the fruits. Although the fruits resemble an achene in size and by having a thin, often leathery mesocarp, they do not conform with the definition of an achene in that the seed coat is not adnate to the pericarp, and under natural conditions the fruits are rarely ever dry. Muenscher (1936), in fact, has shown that when the fruits are subjected to drying, a very high rate of mortality occurs. The fact that the fruits rarely dry also rules out the possibility of their being a nut or nutlet. According to Aalto (1970) the fruits are histologically drupes since the pericarp is differentiated into an exocarp, mesocarp, and stony endocarp. The fruit is, however, unlike a drupe because

the dorsal area of the pericarp wall appears to open and then be covered by a lid (Aalto, 1970). At the junction of the lateral walls and the lid, a ridge is formed. This ridge, in many species, is pronounced into two lateral wings (one on each side of the fruit). The lid can be removed exposing the seed coat. Because of the histological similarity, Aalto chose to call the fruits of the Fennoscandian species drupes. Until a better term is proposed, I am considering the fruits drupe-like.

The fruits are the single most important character for distinguishing the taxa of the *Pusilli*. Several fruit characters are useful for identification: 1) color — usually brown or green; 2) size; 3) shape — whether widest above the middle, at the middle, or below the middle; 4) presence of dorsal or lateral wings or ridges — one species, *P. foliosus*, has a dorsal wing, three others two lateral and one dorsal ridge, others have no ridges; 5) amount of depression on the sides; 6) length and position of the style (or beak).

Aalto (1970) has demonstrated that for some species of *Potamogeton* the endocarp can be useful for identification. The majority of his work was done with subfossil endocarps. He also exposed recent endocarps by boiling the fruits in 5% potassium hydroxide solution for 10 to 15 minutes. The exocarp and mesocarp disintegrate leaving the endocarp exposed. These were examined for shape and size of the cells and for shape, size, and appendages of the endocarp.

VEGETATIVE DIMORPHISM

Vegetative morphology has been used as a basis for separation of certain taxa of *Potamogeton*. In Fernald's study (1932), *P. pusillus* was divided into six varieties based on shape of the leaf apex and number of lacunae bordering the leaf midrib. The species was divided into two informal groups using the shape of the leaf apex. These groups then were further divided into the varieties with the num-

ber of lacunae being the only character used for separation. During the summer of 1878, E. S. Miller made two collections of *P. pusillus* from presumably the same locality of the Wading River, Suffolk County, New York: 1) sterile plants on 25 May 1878, and 2) fertile plants on 12 Jul. 1878. A sterile and fertile plant together were mounted on a herbarium sheet and these sheets were distributed. I have seen six such sheets and on every one the sterile plant had leaves with obtuse apices and two to three rows of lacunae each side of the midribs. Leaves of the fertile specimens, on the other hand, were acute and lacked lacunae. Fernald examined some of the specimens and consistently identified the sterile plants as *P. pusillus* var. *mucronatus* and the fertile plants as *P. pusillus* var. *tenuissimus*. This situation led me to consider the hypothesis that the taxonomic character of the leaf apex and lacunae were environmentally controlled. I, therefore, began visiting populations several times throughout one year and, often, in subsequent years to see if any morphological changes occurred. Data gathered from these field studies indicate that *P. pusillus* and, also, *P. friesii* may undergo a dimorphism in which two morphologically dissimilar phenotypes may be observed in the same population.

During the summer of 1969, I made a collection of *Potamogeton pusillus* (Haynes 3251) from Pelee Island, Ontario. These specimens had obtuse leaves with five to six rows of lacunae on each side of the midrib (Fig. 1). The population was visited separately by Dr. Ronald L. Stuckey and Mr. Marvin L. Roberts, both of The Ohio State University, several times during the next two years. In late August 1971, the population was found in fruit (Roberts 1562). The leaves from this collection were acute and had at most two rows of lacunae each side of the midrib (Fig. 1). Therefore, plants of this one population could be correctly identified, according to Fernald (1932), as var. *mucronatus* when sterile and var. *tenuissimus* when fertile. I also have observed this phenomenon in a population from New York (Haynes 3326). Here both types of leaves were found on

the same plant. The obtuse, lacunate leaves were black and appeared dead at the time of collection and the acute, non-lacunate leaves were green and alive at the time of collection. During the course of herbarium work, I have examined many specimens in which both types of leaves were present on one plant, usually with the obtuse, lacunate ones appearing to have been dead at the time of collection. These data appear to indicate that plants with obtuse lacunate leaves are always sterile. This is not the case. Some are fertile; however, as compared with the number of fertile plants with non-lacunate, acute leaves, the former are few in number.

A similar situation can be observed in *Potamogeton friesii*. However, rather than two distinct sets of leaves being produced by one plant, apparently only one set of leaves is produced a year, but these leaves undergo a morphological change during the growing season. According to Voss (1972), *P. friesii* tends to have leaves without revolute margins, whereas *P. strictifolius* normally has ones with revolute margins. Data gathered during my field work indicate that in the early summer *P. friesii* does have leaves without revolute margins (Fig. 1). A population in Emmet County, Michigan, visited by me on 15 Jun. 1971 (Haynes 3694) had such leaves. However, on 30 Jul. 1971, I again visited the same population and found most plants with leaves having revolute margins (Haynes 3747). Thus, one population may produce both phenotypic expressions in one year.

The two examples of vegetative dimorphism outlined above illustrate the vegetative plasticity of *Potamogeton* explained by Dandy and Taylor (1940). These data indicate that within the *Pusilli*, and probably other groups of aquatic plants, the effects of differing environmental conditions upon the vegetative characters should be understood before one uses these characters in a classification.

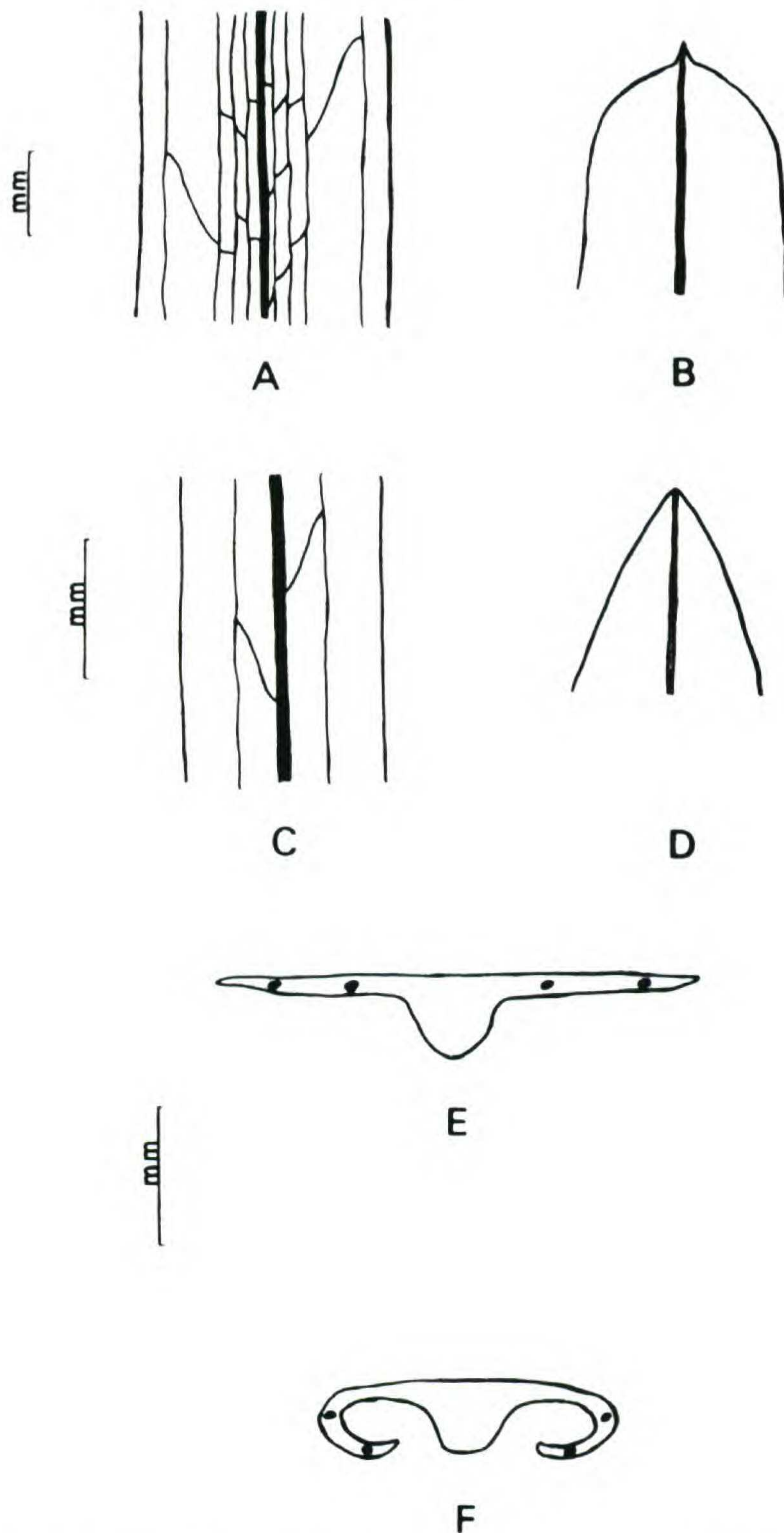


Fig. 1. *Potamogeton pusillus* leaf (A-D). A. Midsection, early summer. B. Apex, early summer. C. Midsection, late summer. D. Apex, late summer. Cross-section of *Potamogeton friesii* leaf (E-F). E. Early summer. F. Late summer.

REPRODUCTIVE ECOLOGY

REPRODUCTION: The reproductive ecology of *Potamogeton* is poorly known. According to Sculthorpe (1967) certain species of *Potamogeton* reproduce by rhizome fragments, tubers, and winter buds or turions. Also, Moore (1915) studied seed germination of *Potamogeton* and concluded that once a seed germinates and develops into a mature plant, several periods of vegetative reproduction must occur before the plant will produce flowers and fruits. In the *Pusilli*, Hagstrom (1916) and Fernald (1932) were of the opinion that the plants rarely reproduced by seeds, but instead, reproduced mostly by winter buds. For the species in which winter buds are rare or unknown, this idea of reproduction by winter buds may not be valid. However, for the species which prolifically produce winter buds, reproduction by these structures is probably the most common type, since fruiting plants often are found with winter buds attached to the underground parts.

POLLINATION: According to Sculthorpe (1967) and to Cronquist (1968), the pollination trend in the Alismatiaceae is from insect to wind, and ultimately, to water pollination. Members of the genus *Potamogeton* including the *Pusilli* are, for the most part, wind pollinated (Sculthorpe, 1967). However, according to Voss (1972) and data based on personal field experience, many inflorescences of the *Pusilli* never become emergent. In such instances, if pollination does occur, the medium for the transport of the pollen must be the water. However, the mature, viable fruits might be formed as a result of apomixis.

GERMINATION: As shown by Muenscher (1936), the germination rate of *Potamogeton* fruits is greatly reduced when the fruits are subjected to drying. Many species, according to Muenscher, require near-freezing temperatures for a period of one to three months. However, as shown by Sullivan (1967) for many of the broad-leaved species of *Potamogeton*, the fruits can be induced to germi-

nate without a previous cold treatment if the exocarp and mesocarp are split, thus exposing the endocarp.

As stated earlier, the fruits of the pondweeds are among the most common foods of waterfowl. Often only the exocarp and mesocarp are digested, leaving the endocarp with the intact seed to be passed from the digestive system. Lohammar (1954) has shown that a high percentage of germination may occur after the fruits have passed through the digestive system of the waterfowl.

CYTOLOGY

Several workers, e.g. Palmgren (1939), Harada (1942; 1956), Löve (1954), Löve and Löve (1961), and Stern (1961), have studied *Potamogeton* cytologically. However, according to Bolkhovskikh *et al.* (1969), these studies have produced chromosome counts for only 50 of the approximately 100 species of the genus. Stern (personal communication) indicates that the pondweeds are difficult to collect for meiotic material since the plants undergo meiosis quite rapidly in very early bud stage. The above-mentioned factor added to the fact that the aquatic environment is a difficult one for field work probably are the major reasons that few cytological studies have been undertaken on the pondweeds. During the summers of 1970, 1971, and 1972, I collected flower buds with the intention of obtaining chromosome counts from meiotic material. The buds were preserved in the usual manner with a 3:1 solution of ethyl alcohol and acetic acid. In some instances, the buds were examined within two or three days of collection; in others, the buds were examined after several months. In all instances I failed to have success in obtaining countable meiotic configurations. Therefore, all counts included in this paper are based upon previous reports in the literature.

According to Stern (1961), the base number for *Potamogeton* is $x = 13$ or 14 . The majority of the chromosome numbers reported for the floating-leaved species are multiples of these figures; e.g. *P. amplifolius* Tuckerm., $n = 26$; *P. gramineus* L., $n = 26$; *P. illinoensis* Morong, $n = 52$

(Stern, 1961). On the other hand, most reports for the submersed-species indicate an n number of 13 or 14. A summary of the reported chromosome numbers for the *Pusilli* is included in Table 1.

These reports of chromosome numbers in *Potamogeton* should be considered with caution, as the nomenclature has been considerably confused and most workers, excluding Stern (1961) and Taylor and Mulligan (1968), did not cite voucher specimens from which the counts were taken.

TABLE 1

Published chromosome numbers for *Potamogeton*
subsection *Pusilli*.

Taxon	Chromosome number
<i>P. berchtoldii</i> Fieber	$n = 13$ (Taylor & Mulligan, 1968)
[<i>P. pusillus</i> var. <i>tenuissimus</i>]	$2n = 26$ (Taylor & Mulligan, 1968)
<i>P. foliosus</i> Raf.	$2n = 28$ (Stern, 1961)
<i>P. groenlandicus</i> Hagstrom	$2n = 26$ (Jørgensen, <i>et al.</i> , 1958)
<i>P. mucronatus</i> Schr.	$2n = 26$ (Palmgren, 1939)
[<i>P. friesii</i>]	
<i>P. obtusifolius</i> M. & K.	$2n = 26$ (Palmgren, 1939)
<i>P. panormitanus</i> Biv.	$2n = 26$ (Palmgren, 1939)
[<i>P. pusillus</i> var. <i>pusillus</i>]	
<i>P. strictifolius</i> Ar. Benn.	$2n = 52$ (Löve, 1954)

PHYLETIC RELATIONSHIPS

GENERIC RELATIONSHIPS: According to Cronquist (1968), *Potamogeton* is classified in the Class Liliatae (monocots), Subclass Alismatidae, Order Najadales, and family Potamogetonaceae. He considers the Alismatidae to be "a near-basal sidebranch, a relictual group which has retained a number of primitive characters." The group

is, therefore, not considered to be in the main line of evolution of the monocots.

In studying the relationships of the Potamogetonaceae with other families of the "Helobiae," Chrysler (1907) came to the conclusion that *Potamogeton* was the most primitive genus of the group and that *Potamogeton*-like organisms gave rise to most of the other genera. He considered the floating-leaved species, especially *P. pulcher* with its submersed leaves very similar to its floating leaves, to be more primitive than the submersed-leaved species. The submersed species were assumed to have been derived from the floating-leaved species as "a stage in the assumption of the aquatic life by the genus." One would conclude that Chrysler considered the Helobiae (Alismatidae) to have been derived from terrestrial species.

Cronquist (1968), on the other hand, considered the primitive monocots to have been derived from a Nymphaeales-like dicot, thus aquatic in origin. He considered the typical parallel-veined leaf of the monocot to be a modified, bladeless petiole. From this modified, flattened petiole, the expanded blade of, say *Sagittaria*, could have been derived by the spreading of the veins farther apart near the tip of the petiole. By applying this concept to *Potamogeton*, one could infer that the floating leaves might have been derived from the submersed leaves by an increase in the amount of tissue between the veins near the tip of the petiole. This would imply that possibly the floating-leaved species were derived from some ancestral stock of submersed-leaved plants.

Published cytological data (cf. cytological section) support this interpretation. The submerged-leaved species are, for the most part, diploid, whereas the floating-leaved species are, for the most part, tetraploid. Although Raven and Thompson (1964), DeWet (1965), and Anderson (1972) have demonstrated instances of polyhaploidy, based upon our present interpretation of cytological data as evidence for evolutionary relationships, the published chromosome

numbers indicate that the primitive condition probably was that of total vegetative submergence.

As stated earlier, pollination in the Alismatidae is of three types — insect, wind, and water. According to Cronquist (1968), the reduction of the perianth in the Najadales reflects the abandonment of insect pollination, with water pollination, as in *Najas* and *Zostera*, being the most specialized type. One would suspect, therefore, the primitive species of *Potamogeton* to be wind-pollinated. The water-pollinated species, then, would have been derived from some wind-pollinated ancestral stock. Again, this interpretation is supported by cytological data. Chromosome number reports for the *P. filiformis* subsection are the highest of all *Potamogeton*. This group is the only one thought to be totally water-pollinated. Palmgren (1939) reports numbers of $2n = \text{ca. } 66$ for *P. filiformis* Pers. and $2n = \text{ca. } 88$ for *P. vaginatus* Turcz.

Based upon the scanty cytological, pollination, and morphological evidence, I here propose that the primitive species of *Potamogeton* were similar to *P. zosterifolius* in that they possessed narrow submersed leaves with many fine nerves and that they were wind pollinated. From the *Potamogeton zosterifolius*-like ancestor, several lines of differentiation probably occurred. One of these, featuring a reduction in vein number and retaining the wind pollination, eventually gave rise to the *Pusilli*. As the scope of this paper is only the *Pusilli*, I will not postulate on the systematic relationships of the entire genus. Instead, my further comments on this subject will be restricted to the *Pusilli*.

SUBSECTIONAL RELATIONSHIPS: *Potamogeton* subsection *Pusilli* is treated here to consist of 15 species. The species morphologically most similar to *P. zosterifolius* is *P. friesii*. The latter species, as does *P. strictifolius*, resembles *P. zosterifolius* in fruits, peduncles, inflorescence, leaves, and stipules. *Potamogeton friesii*, therefore, is probably the most primitive species of the *Pusilli*. *Potamogeton*

strictifolius, being a tetraploid, probably was derived from a *P. friesii*-like ancestor by polyploidy. One can postulate two main lines having developed from the ancestral *Pusilli* (Fig. 2): 1) dorsal and lateral keels absent; 2) dorsal and/or lateral keels present.

The first line is represented by *Potamogeton pusillus* and *P. groenlandicus*. *Potamogeton pusillus* is widespread throughout the world, whereas *P. groenlandicus* is restricted to the coastal areas of Greenland. The latter species probably represents a population of *P. pusillus* that was isolated on Greenland and has differentiated from those of *P. pusillus*.

The second line is represented by *Potamogeton obtusifolius*, *P. hillii*, *P. clystocarpus*, and *P. foliosus*. *Potamogeton foliosus*, having a chromosome number of $2n = 28$, probably represents a population which was separated from a *P. obtusifolius*-like ancestor by aneuploidy and has become widespread. In fact, it is so widely distributed in North America that it is difficult to draw any relationships as to its possible place of origin. However, other species of the line as well as *P. strictifolius* and *P. friesii* have very distinct distributions. These ranges will be discussed and used as supplemental evidence for the phyletic relationships. *Potamogeton obtusifolius*, *P. strictifolius*, and *P. friesii*, have distributions limited almost entirely to geographical areas that were covered with ice during Pleistocene glaciation. These species probably survived glaciation elsewhere and migrated into the once glaciated areas following the retreat of the ice. Apparently, species or varieties could have evolved in a matter of 10,000 years. One need only examine a few of the Great Lakes endemics, e.g. *Iris lacustris* (Guire & Voss, 1963), *Cirsium pitcheri* (Johnson & Iltis, 1963), and *Calamovilfa longifolia* var. *magna* (Thieret, 1960). However, in comparison to these sand dunes endemics, most of the *Pusilli* are wide ranging circumboreal species. If these *Pusilli* were to have evolved recently, then rapid circumpolar dispersal also would have had to occur.

Hultén (1937) proposed that there were two main refugia in North America — the Rocky Mountains and the continental shelf outside eastern America — where plants survived during continental glaciation. From these refugia, he stated, the plants probably spread in an easterly and westerly direction, respectively, toward the center of the continent. Some taxa probably survived in only one area, while other taxa possibly survived in both areas. Some of the taxa which survived in both refugia migrated until their ranges overlapped; thus, they now have a continuous range across North America. For others, however, migration ceased before the ranges overlapped. Hultén conceded that species surviving in other areas south of the glacial boundary did migrate north to some extent into the once glaciated lands. However, he suggested that a much smaller proportion of the species now found in the glaciated areas survived in the vast areas south of maximum glaciation than in the two other refugia.

Iltis (1965) and Stuckey (1972) have suggested that certain species of *Gentianopsis* and *Rorippa*, respectively, survived glaciation in the Rockies and migrated eastward following the retreat of the Wisconsin Ice sheet. The distributions of the taxa discussed by these two workers are similar to that of *Potamogeton obtusifolius*, *P. strictifolius*, and *P. friesii* in that all have a more or less continuous range across northern North America and are mostly known from south of the glacial boundary only in the Rockies. Marie-Victorin (1938) proposed an explanation of the eastward migration of such species by suggesting that “the unforested belt that must have existed along a receding icefront [served] as a kind of sidewalk extending from the Rockies to the Gulf of St. Lawrence.” He cited no pondweeds which demonstrated such distributions, but Stuckey (1972) indicated that *P. friesii* and *P. strictifolius* have ranges similar to a distribution pattern that Marie-Victorin probably had in mind when proposing this idea.

At the time of Hultén’s article (1937) *Potamogeton obtusifolius* from western America was represented by few

collections, all from localities in glaciated areas. This exiguous number of specimens from western America led Hultén to regard the taxon as a circumpolar species which survived in the eastern refugium. However, recent collections indicate that the taxon is widespread, although uncommon, throughout this geographical area, including the Rocky Mountains. Therefore, I include *P. obtusifolius* as a taxon which survived continental glaciation in the western refugium and then migrated eastward.

Potamogeton hillii, on the other hand, survived continental glaciation in eastern America just south of the glacial boundary, in the area of Pennsylvania, and migrated north and west with the retreat of the ice. In fact, the morphological similarity of the species with *P. obtusifolius* would indicate that prior to glaciation, the two currently recognized taxa were perhaps represented by one large heterogeneous population. Glaciation would have separated this large population into two smaller allopatric ones, one to the east and one to the west. During glaciation, the two populations differentiated, resulting in each population evolving into a different species. Once the period of glaciation was complete and the distributions overlapped, the reproductive barriers that had been established during glaciation, evidently now prevents gene flow from one population to the other. Iltis (1965) indicated that *Gentianopsis procera* and *G. crinita* possibly had a similar history. Similarly, *P. clystocarpus* is known from only one locality in Jeff Davis County, Texas. This species probably represents a population of *P. obtusifolius* in the southern mountains which was isolated and has differentiated from the parental population.

TAXONOMY

Of the more than 60 names that have been proposed for the North American *Potamogeton* subsection *Pusilli*, most of these are based on differences in venation, texture, color, lacunae number, and apex shape of the leaves. Dandy (1937), Dandy and Taylor (1940), and Clapham *et al.*

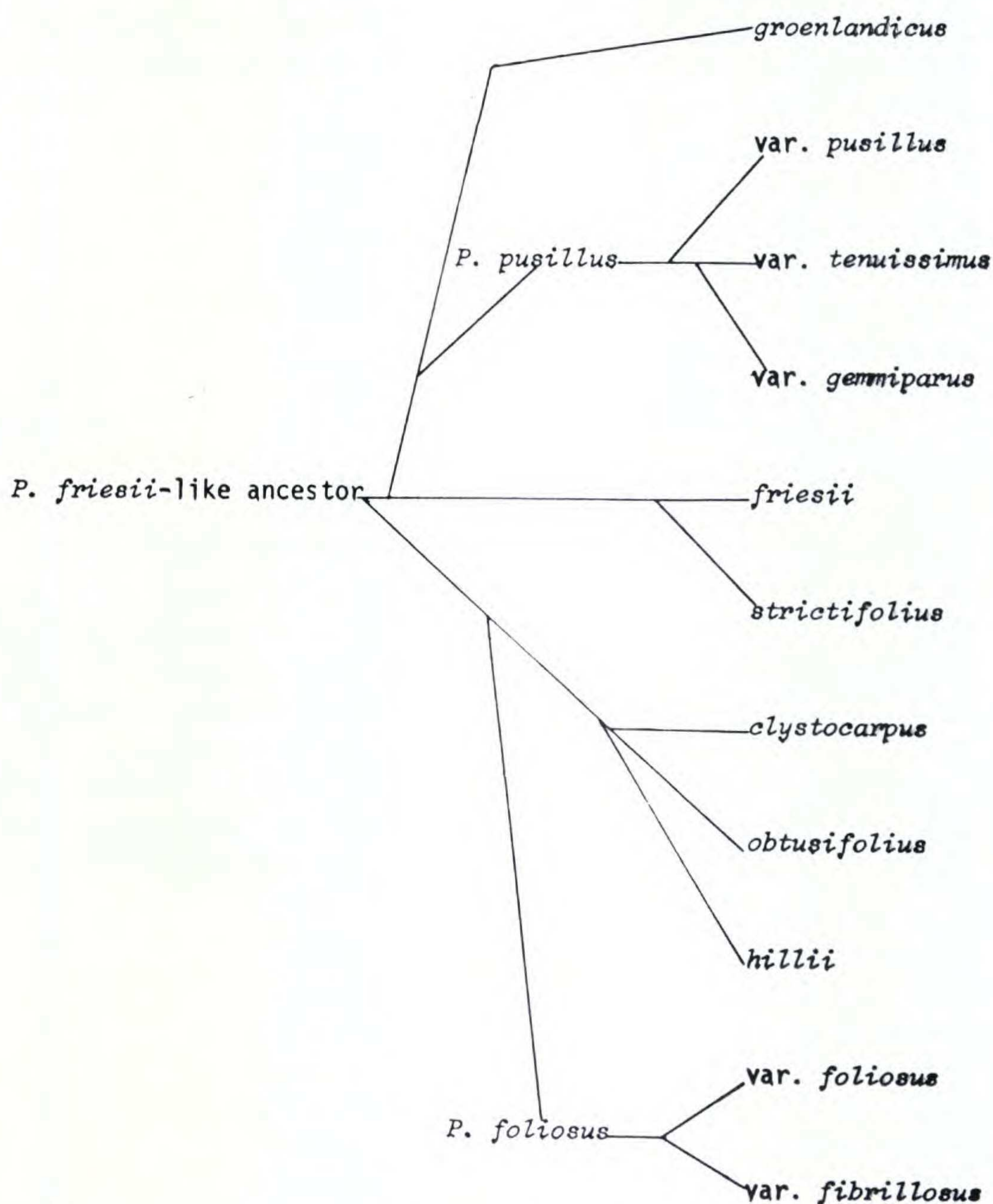


Fig. 2. Hypothetical phylogenetic relationships of North American *Pusilli*.

(1962) have shown that the leaf form and anatomy of *Potamogeton* may vary widely with age, water depth, current speed, nutrient supply, light intensity, and perhaps other factors. Data from classical and experimental studies of other genera of aquatic vascular plants indicate that this

heterophyllous condition is common among the submerged species. Fassett (1951) illustrated no fewer than ten quite distinct individuals of *Callitriche heterophylla* and drew attention to the close morphological similarities of ecological forms which actually belong to different species. Bostrack and Millington (1962) found in *Ranunculus flabellaris* that the shape of the leaf may be affected by temperatures, photoperiod, light intensity, and submergence acting directly upon the distribution and frequency of cell division in the primordium so that the inherent zones of growth initiated on the primordium are modified in their development. Cook (1966), in fact, after recognizing 20 taxa of *Ranunculus* subgenus *Batrachium* listed 302 names which applied to these taxa. Williams (1970) found that by transplanting individuals of *Nymphaea tuberosa* to localities where *N. odorata* occurred, the individual would lose its "*tuberosa*" characters and obtain those of *N. odorata*. For reasons just outlined, these workers have found it necessary to compile a classification based primarily on reproductive characters.

My approach to the systematics of *Potamogeton* subsection *Pusilli* has been primarily that of combined herbarium and field studies. The data presented are based on three summers field work in northern United States and southern Canada and an examination of over 8000 herbarium specimens from the following 22 herbaria (Acronyms from Langjouw and Stafleu, 1964): C, CAN, CGE, DAO, F, GH, ILL, K, LAF, MICH, MO, MU, NY, NYS, OS, PH, S, UC, UMBS, UPS, US, W.

Evidence from the field work has indicated that the *Pusilli* are as morphologically plastic as *Callitriche* and *Ranunculus*. Just as workers in these other genera have resorted to fruiting characters as a basis of a classification, I think that a classification based for the most part upon the reproductive structures is the only one which would be workable. Therefore, one should always attempt to collect flowering or fruiting specimens (preferably fruiting)! Just as identification of a sterile *Aster* or *Solidago* is nearly impossible, it is difficult at best to identify a sterile pondweed (and then one can never be sure of his determination).

I have thus refrained from mapping any specimen in which the determination was questionable.

For one to completely adhere to the biological species concept, he should demonstrate, either experimentally or naturally, if hybridization between two taxa does occur. However, in genera such as *Potamogeton*, in which the flowers are so small as to render difficult the artificial crossing of individuals, one hardly can demonstrate whether two individuals are capable of crossing and producing fertile offspring. Ogden (1943) has suggested that the broad-leaved species of *Potamogeton* hybridize quite readily. He, however, did not demonstrate this phenomenon experimentally; rather he depended wholly upon the hybrid individuals possessing characters intermediate between those of the two putative parents. With the *Pusilli*, however, it is not so easy. Vegetatively, the condition one would expect to find a hybrid, the species of the *Pusilli* are quite similar; thus, intermediates would be difficult to detect. Therefore, the techniques used by Ogden are not applicable to the *Pusilli*.

Because of the difficulties outlined above with hybridization, I have chosen to stress a morphological species concept. I have followed the premise that species should be separated by discontinuities between the morphological ranges of the fruits, peduncles, inflorescence, and, to a lesser extent, the winter buds. Therefore, for the 60 names which have been applied to the North American *Pusilli*, I am accepting only eight species, with one of these, *Potamogeton foliosus*, being represented by two varieties and another, *P. pusillus*, being represented by three varieties. In an attempt for consistency, I have regarded varieties as morpho-geographic subdivisions of a species (Kapadia, 1964) that presumably reflect genetic differences. As will be noticed, I do not recognize subspecies or forms. It is my contention (as that of Raven, 1969) that only one infraspecific unit should be recognized. I have chosen to use variety over subspecies because of tradition in eastern North America.

In the treatment that follows, keys are based upon fruiting material. Dimensions of leaves are taken from the fully expanded, longest leaves of a specimen. Measurements of the width were taken approximately at the widest point of the leaf. Dimensions of the spike and peduncles are based upon both flowering and fruiting specimens. Descriptions of the fruits are taken strictly from mature structures.

POTAMOGETON Linnaeus, *Species Plantarum* 126. 1753

Hydrogeton Loureiro, *Flora Cochinchinensis* 244. 1790.
Type Species: *Hydrogeton heterophyllum* = *Potamogeton octandrus* Poir.

Patamogeton Honckeny, *Syn. Plan. Germ.* 2: 110. 1793.
(orthographic variant).

Potamogiton Rafinesque, *Med. Repos.* 5: 354. 1808. (orthographic variant).

Potamogetum Clairville, *Man. d'Herb. Suisse & Valais* 34. 1811. (orthographic variant).

Peltopsis Rafinesque, *J. Phys. Chim. Hist. Nat. Arts* 89: 102. 1819. Type Species: *Potamogeton perfoliatus*. L.

Spirillus J. Gay, *Compt. Rend. Hebd. Seances Acad. Sci.* 38: 703. 1854. (name without any listed species); emend. Nieuwland, *Amer. Midl. Naturalist* 3: 14. 1913. Type Species: (lectotype here designated) *Potamogeton diversifolius* Raf.

Plants herbaceous, aquatic, submerged in fresh or rarely brackish water, annual or perennial, propagated from seeds, winter buds, or rhizomes. Stems variable in length according to water depth, branched or unbranched, terete or compressed, rooting at the nodes. Leaves all submersed or both submersed and floating, alternate or subopposite; submersed leaves pellucid, sessile or petiolate, linear to orbicular, subulate to obtuse at the apex, the margins entire to serrate, rarely crimped, the nerves 1-35; floating leaves coriaceous, mostly petiolate, rarely subsessile, elliptic to

ovate, acute to obtuse at apex, cuneate to rounded or cordate at base, the margins entire, the nerves 3-51. Stipules tubular, sheathing the stem and young inflorescences, connate or convolute, either free or adnate to the base of submersed leaves, free from base of floating leaves. Winter buds present or absent, with extremely shortened nodes, divided into inner and outer leaves; inner leaves few to numerous, either shortened and oriented at 90° angles with respect to outer leaves, rolled into a fusiform structure, or unmodified; outer leaves 1-5 per side, mostly similar to vegetative leaves, rarely corrugated near base. Inflorescence a capitate or cylindric spike with 1 to 20 whorls of flowers, compact or moniliform, with 2 to 4 flowers each whorl, mostly buoyed above surface of water. Flowers bisporangiate. Perianth of 4, free, rounded, short-clawed, greenish segments. Androecium of 4 stamens: filaments adnate to the perianth claw; anthers bithecate, extrorse. Pollen spherical monoaperturate. Gynoecium of 4, free, unilocular, uniovulate carpels; ovule campylotropus; placentation parietal. Fruit drupe-like; dorsally rounded or keeled; embryo coiled; cotyledon one, endosperm absent. Chromosome base number: $x = 13$ or 14 (Stern, 1961). (Name from the Greek *potamos*, a river and *geiton*, a neighbor.) Type Species: *Potamogeton natans* L. (*fide* Taylor, 1909).

POTAMOGETON Subsection **PUSILLI** Graebn. in Aschers. & Graebn. Das Pflanzenreich 4(11): 260. 1907.

Plants submersed in fresh water, annual or perennial. Stems branched or unbranched, terete or compressed. Leaves all submersed, pellucid, sessile, linear, subulate to obtuse at apex, entire, 1-9-nerved. Stipules connate or convolute, free from the base of the leaves. Winter buds present or absent. Inflorescence mostly emergent, a capitate or cylindric spike with 1-5 whorls of flowers, compact or moniliform, mostly with 4 flowers at each whorl. Fruit dorsally rounded or keeled, to 4.0 mm long. Chromosome base number $x = 13$ or 14 . Type Species: *Potamogeton pusillus* L.

KEY TO THE TAXA OF NORTH AMERICA

1. Leaves 7-9-nerved *and* inner-leaves of winter buds unmodified; plants of Greenland. ... 8. *P. groenlandicus*.
1. Leaves with up to 9 nerves, but *if* 7-9-nerved, *then* with inner-leaves of winter buds modified; plants from areas other than Greenland. 2.
2. Fruits with a dorsal keel or ridge to 0.4 mm high, often with 2 lateral keels. 3.
3. Inflorescence cylindric, 8 mm or more long; basal glands usually present, mostly 0.5 mm or larger in diam; leaves obtuse or apiculate, rufescent. 3. *P. obtusifolius*.
3. Inflorescence capitate or rarely cylindric, 7.5 mm or shorter; basal glands when present, mostly smaller than 0.5 mm diam; leaves acute, rarely obtuse, olive or green. 4.
4. Peduncle cylindric, mostly terminal, erect; basal glands present; fruit with basal tubercles. 6. *P. clystocarpus*.
4. Peduncles usually clavate, axillary, often recurved; basal glands uncommon; fruit without basal tubercles. 5.
5. Fruits rounded on sides, 3-keeled, 3-4 mm long; dorsal keel ridge-like, to 0.2 mm high. 4. *P. hillii*.
5. Fruits with concave sides, 1-keeled, to 2.7 mm long; dorsal keel wing-like and undulate, to 0.4 mm high. 6.
6. Spike rarely interrupted; fruit olive to green-brown, 1.5-2.7 mm long, 1.2-2.2 mm wide; keel mostly 0.2 mm high or higher; beak 0.2-0.6 mm long; stipular veins decaying with age; basal glands rare, to 0.3 mm diam. 5a. *P. foliosus* var. *foliosus*.

6. Spike mostly interrupted; fruit pale-green, 1.4-1.7 mm long, 1.1-1.2 mm wide; keel mostly less than 0.2 mm high; beak 0.2 mm long or less; stipular veins with age remaining as long fibers; basal glands common, to 0.5 mm diam. . . 5b. *P. foliosus* var. *fibrillosus*.
2. Fruits with dorsal surface rounded; lateral keels absent. 7.
7. Stipules more or less coarsely fibrous, whitish, the oldest tending to disintegrate into shreds; bases of winter-buds usually indurated and corrugated; peduncles mostly clavate. 8.
8. Leaf tips rounded to apiculate; leaves light green to rufescent, 5-7 (-9)-nerved, 1.2-3.2 mm wide; winter buds 1.5-4.0 mm wide, inner leaves modified into a fan-shaped structure, outer leaves corrugated at base; peduncles compressed; stem compressed. . 1. *P. friesii*.
8. Leaf tips acute, rarely obtuse, mostly deep green to olive, 3-5 (-7)-nerved, 0.6-2.0 mm wide; winter buds 0.8-2.2 mm wide; inner leaves modified into a fusiform structure, outer leaves rarely with corrugations at base; peduncles mostly terete; stem mostly terete. 2. *P. strictifolius*.
7. Stipules mostly delicate, whitish, green, or brownish, usually disintegrating with age; bases of winter-buds without corrugations; peduncles cylindric. 9.
9. Fruits 2.5-3.6 mm long, 1.7-2.4 mm wide; winter buds 3.5-7.8 cm long, 2.3-5.1 mm wide, inner leaves unmodified. . . 3. *P. obtusifolius*.
9. Fruits 1.5-2.2 mm long, 1.2-1.6 mm wide; winter buds 0.9-3.2 cm long, 0.3-1.8 mm wide, inner leaves modified into a fusiform structure. 10.

- 10. Leaves uninervate, subulate, 0.2-0.7 mm wide; plants of New England and southern Quebec. 7c. *P. pusillus* var. *gemmiparus*.
- 10. Leaves 1-5-nerved, acute to obtuse, 0.2-2.5 mm wide; widespread throughout North America. 11.
- 11. *Mature* fruit widest above the middle, sides concave, beak central; peduncle filiform to cylindrical, usually 1-3 per plant; inflorescence usually of 2-4 distinct verticels; leaves with up to 2 rows of lacunae along midrib, apex acute, rarely apiculate; stipules mostly connate. 7a. *P. pusillus* var. *pusillus*.
- 11. *Mature* fruit mostly widest at or below the middle, sides rounded, beak mostly forward, peduncles cylindrical, usually more than 3 per plant; inflorescence mostly of 1-2 adjacent verticels; leaves with 1-5 rows of lacunae along midrib, apex acute to obtuse; stipules mostly convolute. 7b. *P. pusillus* var. *tenuissimus*.

1. **Potamogeton friesii** Rupr. in Beitr. Pflanzenk. Russ. Reiches 4: 43. 1845. TYPE: (type not located), application of the name is from the illustration of *Potamogeton compressus* auct. non Linn.: In Reichenbach. Icones Florae Germanicae et Helveticae 7: pl. 24. 1845!

Spirillus friesii (Rupr.) Nieuwl. Amer. Midl. Naturalist 3: 17. 1913.

Potamogeton pusillus var. *major* Fries, Novitiae Florae Suecicae, ed. 2, 48. 1828. *P. mucronatus* Schr. ex Sonder, Flora Hamburgensis 99. 1851. *P. major* (Fries) Morong, Mem. Torrey Bot. Club 3: 41. 1893. TYPE: (type not lo-

cated), application of the name is from the illustration of *Potamogeton compressum* auct. non L.: In Smith, English Bot. 2: pl. 418. 1797!

Potamogeton pusillus var. *latifolius* Meyer, Chloris Hanoverana, 525. 1836. *P. oederi* Meyer, Flora Hanoverana Excursoria 536. 1849. TYPE: (type not located), application of the name is from the illustration of *Potamogeton compressum* auct. non L.: In Oeder, Flora Danica 2: (4) t. 203. 1765!

Stem pale green to pale brown, simple to profusely branched near the apex, compressed, slightly ridged, 10-135 cm long, 0.3-1.1 mm diam. Leaves usually light green, rarely olive-green to rufescent, delicate to rigid, 5-7 (-9)-nerved, 2.3-6.5 cm long, 1.2-3.2 mm wide; apex acute to apiculate, glands green, greenish-brown, or gold, to 0.7 mm diam; lacunae absent or 1 narrow row each side of the midrib; lateral nerves joining the midrib 0.2-0.9 mm below the apex. Stipules white, fibrous, shredding at apex, 5.5-21.0 mm long, 0.7-2.5 mm diam. Winter buds common, terminal or lateral, 1.5-5.0 cm long, 1.5-4.0 mm wide; inner leaves reduced, arranged into a fan-shaped structure and oriented at right angles to the outer leaves; outer leaves 2-3 per side, apiculate to acute, corrugated at base. Peduncles usually slightly clavate, terminal or axillary, rarely recurved, 1.2-4.1 (-7.0) cm long, (0.1-) 0.5-1.2 mm diam. Spike cylindrical, 7.0-16.0 mm long, 2.6-8.0 mm diam; verticels 2-5, 1.5-5.0 mm apart. Perianth segment 1.2-1.5 mm long, 0.5-1.5 mm wide. Fruit olive-green to brown, without dorsal keel, 1.8-2.5 mm long, 1.2-2.0 mm wide; beak central, 0.3-0.7 mm long, 0.2-0.5 mm diam; sides rounded, rarely centrally depressed; wall texture smooth, rarely reticulate. Chromosome number, $2n = 26$ (Palmgren, 1939).

Distribution: Central Alaska to Newfoundland, south to northeastern Utah and southeastern Pennsylvania, Fig. 3. Fruiting from late June to September.

Illustrations: Fernald (1932, pl. 6; 29, fig. 3; 33, fig. 1; and 39, fig. 8).

Nomenclaturally, *Potamogeton friesii* has been poorly understood. The taxon was long referred to *P. compressum* L. (Smith, 1797; Oeder, 1765; Reichenbach, 1845). Fries (1828) regarded the taxon as a variety of *P. pusillus* and, therefore, proposed *P. pusillus* var. *major*. However, Mertens and Koch (1828) had made the same combination for a different taxon. Thus, Fries' name was a later homonym. The first combination at specific rank which apparently applied to this entity was *P. mucronatus* Schrader. However, to my knowledge, this name was never published by Schrader, but first appeared in Romer and Schultes (1818) as a *nomen nudum* — "Qid *P. mucronatus* Schrader." I have been unable to locate the name again until used by Reichenbach (1845), definitely placing the name in synon-

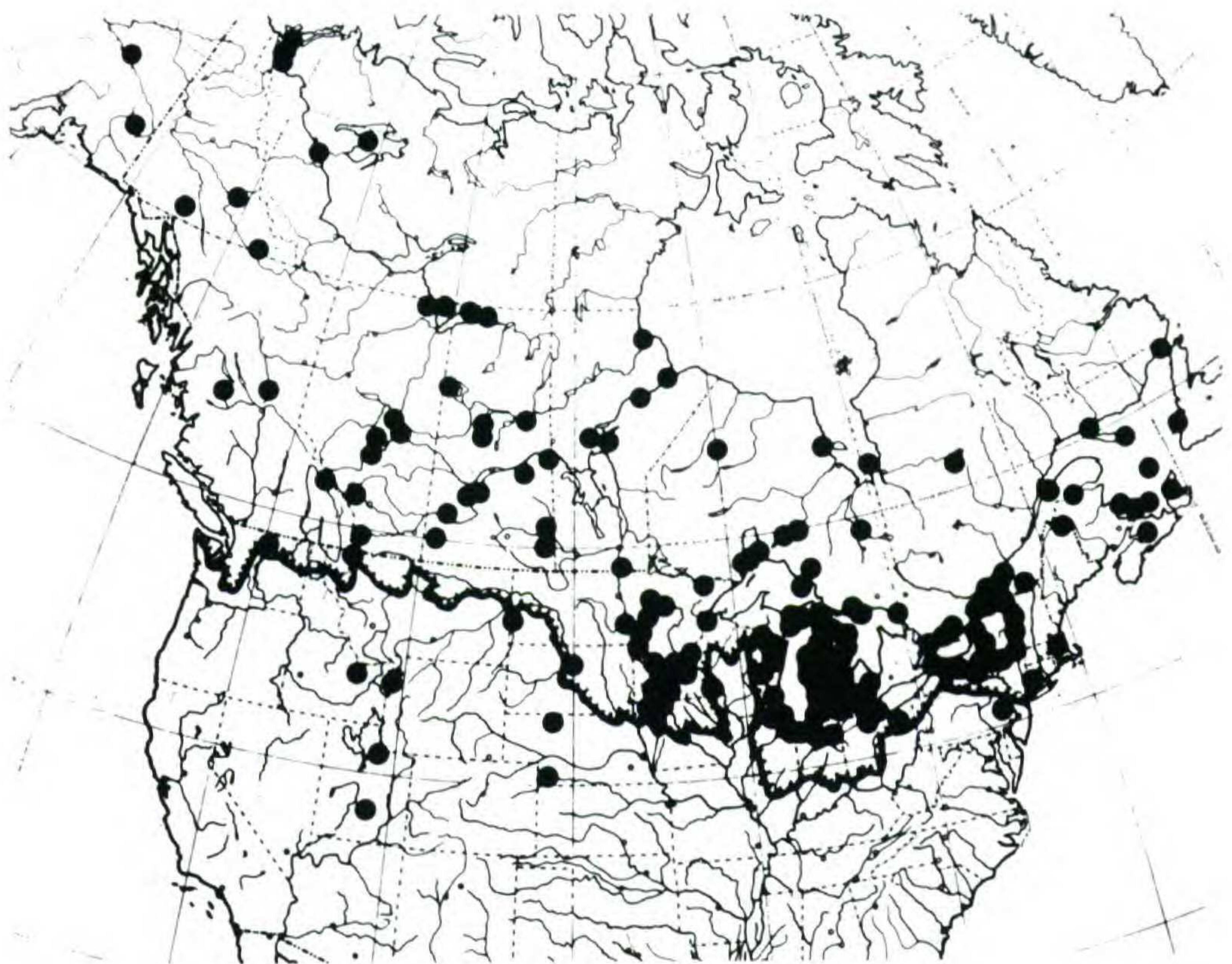


Fig. 3. Map of North America showing the documented distribution of *Potamogeton friesii*. The barred line represents the southern limit of Wisconsin Glaciation in the United States east and west of the Rocky Mountains (after Flint, 1957; Flint, *et al.*, 1959).

omy under *P. compressum* — “*P. mucronatus* Schrader, R. S. III. p. 517!” Neither of these references to *P. mucronatus* constitute publication, since a name is not considered validly published when it originally appears in synonymy. Apparently, the name was not validly published in specific rank until Sonder (1851) applied a description, giving credit to Schrader.

However, Ruprecht (1845) had validly published *Potamogeton friesii* and accurately applied the name to the entity which we now consider to be this taxon. Although I have not seen any of his original specimens, he referred to the illustration cited above in Reichenbach (1845) and also to one in Oeder (1765), both of which are *Potamogeton friesii*.

REPRESENTATIVE SPECIMENS

CANADA: **Alberta:** Bow River Valley, *Brown* 692 (GH, NY, PH); Banff (Vermilion Lakes), *Malte & Watson* 961 (CAN, GH). **British Columbia:** Blackwater Lake, ca. 32 mi. N. of Golden, *Hitchcock & Martin* 7645 (NY, UC). **Manitoba:** Cross Lake, 45 mi N of Lake Winnipeg, *Scoggan* 3573 (CAN). **New Brunswick:** Tidehead, near Campbellton, *Malte* 784 (CAN). **Newfoundland:** St. George's Pond, near Bay St. George, *Fernald & Wiegand* 2456 (CAN, GH, PH, NY). **Northwest Territories:** MacKenzie River delta, East branch, 68°40'N, *Porsild* 7243 (GH, US). **Nova Scotia:** GOLDCHESTER CO.: Salmon River, Truro, *Bissell & Linden* 19698 (GH). **Ontario:** HASTINGS CO.: no locality, *Macoun* s.n. (F, K, MO, NY, S); Charlton Island, James Bay, 52°N, 79°30'W, 4292 (CAN, US, photo at DAO). **Prince Edward Island:** KINGS CO.: Black Pond, *Fernald & St. John* 6772 (CAN, GH, K, NY, US); Cove Head, *Macoun* 3000 (CAN, GH, K, MO, NY). **Quebec:** Coffin Island, Magdalen Islands, *Fernald et al.* 6775 (CAN, GH, K, NY, PH, US); Ile de la Grand-Entree, Magdalen Islands, *Marie-Victorin & Rolland-Germain* 9921 (F, GH, NY, PH, US). **Saskatchewan:** Barrier River, ca. 4 mi. W, 3 mi. S. of McKague, *Breitung* 414 (CAN, DAO, NY, UC). **Yukon:** Craig Lake, vicinity of Carcross, *Porsild* 18418 (CAN). UNITED STATES: **Alaska:** vicinity of College, near Fairbanks, *Argus* 1097 (DAO). **Connecticut:** NEW HAVEN CO.: Derby, *Robbins* (GH, NY). **Idaho:** JEFFERSON CO.: Mud Lake, *Sperry & Martin* 670 (US). **Illinois:** COOK CO.: South Chicago, *Hill* 79-1881 (ILL). **Indiana:** WHITLEY CO.: Goose Lake, ca. 7 mi. NW of Columbia City, *Deam* 48794 (GH). **Iowa:** DICKINSON CO.: East Lake Okoboji, *Shimek* (DAO, F, GH, MO). **Maine:** AROOSTOOK CO.: Washburn, Aroo-

stook River, *Ogden & Chamberlain* 2692 (OS). **Massachusetts:** MIDDLESEX CO.: Fresh Pond, Cambridge, *Faxon* (GH, NY, US). **Michigan:** CHEBOYGAN CO.: Black River between mouth and Alverno, *Haynes* 3377 (LAF, OS); *Haynes* 3385 (MO, OS); *Haynes* 3698 (MO, NY, OS); Hook Point, Douglas Lake, *Haynes* 3361 (F, GH, MO, NY, OS, PH, UC, US); mouth of Bessey Creek, Douglas Lake, *Haynes* 3887 (OS); Marl Bay, Douglas Lake, *Haynes* 3711 (ASU, GH, LAF, OS). EMMET CO.: small arm of Carp Lake, *Haynes* 3376 (OS); *Haynes* 3694 (OS); *Haynes* 3747 (OS); *Haynes* 3889 (OS). MANISTEE CO.: Little Manistee River, Manistee, *Hill* (F, GH, ILL, MO, US). **Minnesota:** CASS CO.: Cullen Lake, *Ballard* (ILL, MICH, MO, UC, US). MARTIN CO.: Silver Lake, *Cratty* (GH, ILL, MO, NY, PH, UC, US). **Montana:** GLACIER CO.: marshes above Lower Two Medicine Lakes, Glacier National Park, *Maguire* 482 (GH). **Nebraska:** CHERRY CO.: Dewey Lake, near Valentine, *Tolstead* 477 (GH). **New York:** CORTLAND CO.: Upper York Lake, near Little York, *Haynes* 3347 (MICH, MO, OS, US); *Haynes* 3348 (F, GH, MO, NY, OS, PH, UC, US); *Haynes* 3349 (MICH, OS); *Haynes* 3350 (MICH, OS). ONTARIO CO.: Lake Seneca, Geneva, *Morong* (CAN, GH, NY, S). SARATOGA CO.: Saratoga Lake, *Haynes* 3311 (MICH, MO, OS). WARREN CO.: Dunham Creek near S. end of Lake George, *Haynes* 3330 (GH, MICH, MO, OS, UC, US); *Haynes* 3331 (MICH, MO, OS, US). **North Dakota:** CASS CO.: Fargo, *Whitney* (MU). **Ohio:** ERIE CO.: East Bay, Sandusky, *Osburn & Williamson* (GH). **Pennsylvania:** LEHIGH CO.: Bethlehem, *Noble* (GH, PH). **South Dakota:** FAULK CO.: ponds and rivers, near Jacques, *Geyer* (US). **Utah:** SUMMIT CO.: Lyman Lake, Blacksfork Creek, *Hobson* 52 (GH). **Vermont:** ADDISON CO.: Little Otter Creek, Ferrisburg, *Faxon* (GH, US). **Washington:** OKANOGAN CO.: Bonaparte Lake, *St. John, et al.* 5298 (GH, MO, UC). **Wisconsin:** BROWN CO.: Point Sable, Green Bay, *Schuetz* (F, GH, K, MICH, UC). MILWAUKEE CO.: Milwaukee, *Lapham* (GH, K, MO, PH). **Wyoming:** TETON CO.: shallow lake, 10 mi. s. of Moran, *Porter & Porter* 7869 (DAO, UPS, UC).

2. *Potamogeton strictifolius* Ar. Benn. J. Bot. 40: 148. 1902.

Potamogeton pusillus var. *pseudo-rutilus* Ar. Benn. J. Bot. 39: 201. 1901. *P. foliosus* × *P. rutilus*? Hagstrom, Kongl. Svenska Vetenskapsakad. Handl. 55(5): 91. 1916. *P. strictifolius* var. *typicus* Fern., Mem. Amer. Acad. Arts 17: 56. 1932. TYPE: *E. J. Hill* [146], Wolf Lake, Hammond, [Lake Co.] Indiana, 3 Sept. 1900, (lectotype, *fide* Fernald, 1932, at K, but not located; photo of lectotype, CAN! NY!, isotype, ILL!).

Potamogeton strictifolius var. *rutiloides* Fern. Mem. Amer. Acad. Arts 17: 57. 1932. *P. pusillus* var. *rutiloides* (Fern.) Boivin, Naturaliste Canad. 94: 527. 1967. TYPE: *F. P. Metcalf* 1453, Molly Lake, 10 mi. N of Brainerd, Crow Wing Co., Minnesota, 26 Aug. 1921, (holotype, GH!; isotype, US!).

Stem pale green to green-brown, branched or simple, more or less rounded, slightly ridged, 27-95 cm long, 0.4-0.8 mm diam. Leaves green to olive, usually rigid, 3-5 (-7)-nerved, 1.2-6.3 cm long, 0.6-2.0 mm wide; apex acute to nearly bristle-tipped; glands white, green, greenish-brown, or gold, to 0.3 mm diam; lacunae usually absent; lateral nerves joining the midrib 0.8-1.5 mm below the apex. Stipules usually white, fibrous, shredding at tip, connate, 0.6-1.6 cm long, 0.6-2.0 mm diam. Winter buds common, terminal or lateral, 2.5-4.8 cm long, 0.8-2.2 mm wide; inner leaves undifferentiated; outer leaves 3-4 per side, acute, mostly without, rarely with, corrugations at base. Peduncles usually cylindric, rarely slightly clavate, terminal, mostly erect, rarely recurved, 1.0-4.5 cm long, 0.3-0.9 mm diam. Spike cylindrical, 0.6-1.3 cm long, 1.5-5.2 mm diam; verticels 3-4, 1.5-3.2 mm apart. Perianth segments 0.9-1.7 mm long, 0.8-1.5 mm wide. Fruit green-brown, without dorsal or lateral keels, 1.9-2.1 mm long, 1.3-1.8 mm wide; beak central, 0.3-0.5 mm long, 0.2-0.4 mm diam; sides rounded, often centrally depressed; wall texture smooth. Chromosome number, $2n = 52$ (Löve, 1954).

Distribution: Northwestern Northwest Territories to eastern Quebec, south to northeastern Utah and northwestern Connecticut. Fruiting from early July to late September. Fig. 4.

Illustrations: Fernald (1932, pl. 7; 8; 29, fig. 4, 5; and 33, fig. 2, 3).

Bennett, in the original description of *Potamogeton pusillus* var. *pseudo-rutilus*, cited two collections: "Lake Scugog, Ontario, Canada, 1897, W. Scott, ex Prof. Macoun;" and

"Wolf Lake, Indiana, U.S.A., 1900, Rev. E. J. Hill." After receiving more material from Hill, Bennett later raised the taxon to specific rank. Hagstrom (1916) examined additional material sent to him by Hill and ascertained this to be a hybrid between *P. foliosus* and *P. rutilus*. Hagstrom cited the original specimen as being from Lake George, East Chicago, rather than from Wolf Lake. I think Hagstrom made an error in citing this specimen, or possibly Lake George and Wolf Lake refer to the same lake. The original most certainly was from Wolf Lake. Hagstrom did not examine material from Lake Scugog, but based his decision on the 1902 description of *P. strictifolius* by Bennett and other Canadian material he had examined from Sea-Cow-Pond, Crane Lake, Assiniboia, Picanok River, Quebec, and Ottawa River, Quebec [which he said "seem excellently to answer to the description of the fruiting plant of Lake Scugog"]. He concluded that the Lake Scugog material was probably the same as *P. panormitanous* (*P. pusillus* var. *pusillus*). Fernald examined Bennett's collection but overlooked the point of whether the Lake Scugog plant was the same taxon as the Wolf Lake plant. As he could not be certain that the two were the same, he did not deny or accept Hagstrom's decision. He did, however, designate Hill's collection from Wolf Lake, Indiana, September 3, 1900, as the Type [lectotype] of *P. strictifolius*. Fernald did say, with which I concur, that Hagstrom had erred in calling *P. strictifolius* a hybrid of *P. foliosus* and *P. rutilus*.

I also am unable to state with assurance that the specimen from Lake Scugog is conspecific with the one from Wolf Lake. I have corresponded with curators of the herbaria (K, BM, & CGE) where the majority of Bennett's material is located. There is no sheet in Bennett's collection at these herbaria filed under *Potamogeton pusillus*, *P. berchtoldii*, or *P. strictifolius*. As I have photographs from CAN, NY, & US of a sheet with only the two specimens mounted on it, I am certain that it is not correctly filed under the name of another specimen on the same sheet. The photograph from CAN has a paragraph in Bennett's handwriting

stating that the sheet was in his collection and that the photograph was taken by his daughter.

I have, however, located a duplicate of Hill's collection from Wolf Lake, and also a second specimen collected by Scott at Lake Scugog on 3 August 1897 (the same day as the one in Bennett's collection). I can not ascertain if Scott's collection is a duplicate of the one sent to Bennett. With its convolute stipules, characteristic winter buds, and one row of lacunae along each side of the midrib, this specimen is rather characteristic of *P. pusillus* var. *tenuissimus*. It is, however, unusual in that the stipules are white rather than the usual greenish-brown of *P. pusillus* var. *tenuissimus*. Until the specimen in Bennett's collection can be located, I am following Fernald in that I cannot be sure to which taxon the Lake Scugog collection should be referred.

Fernald (1932) separated *Potamogeton strictifolius* into two varieties, var. *strictifolius* & var. *rutiloids*, based on the leaf apex shape, rigidity of the leaves, and the coarseness of the stipules. After examining many sheets and hundreds of plants in the field, I have concluded that this variability is both within and between populations. The leaf tips of the isotype of var. *strictifolius* at ILL, for example, vary from very gradually tapering acute to obtuse. Because of this variability within populations and of no apparent range distinctions, I consider *P. strictifolius* to be one taxon. The rigidity of the leaves, I believe to be of ecological rather than of genetic origin.

Morphologically, *Potamogeton strictifolius* is most similar to *P. friesii*. The best way to distinguish the species is by the winter buds. In *P. strictifolius*, the inner leaves of the winter buds are only slightly modified, whereas in *P. friesii* the inner leaves are much shorter than the outer leaves and are oriented at 90° to the outer leaves. Differences in the leaves are difficult to assess. Fernald (1932) and Ogden (personal communication) stress the number of veins — three to five in *P. strictifolius* and five to seven in *P. friesii*.

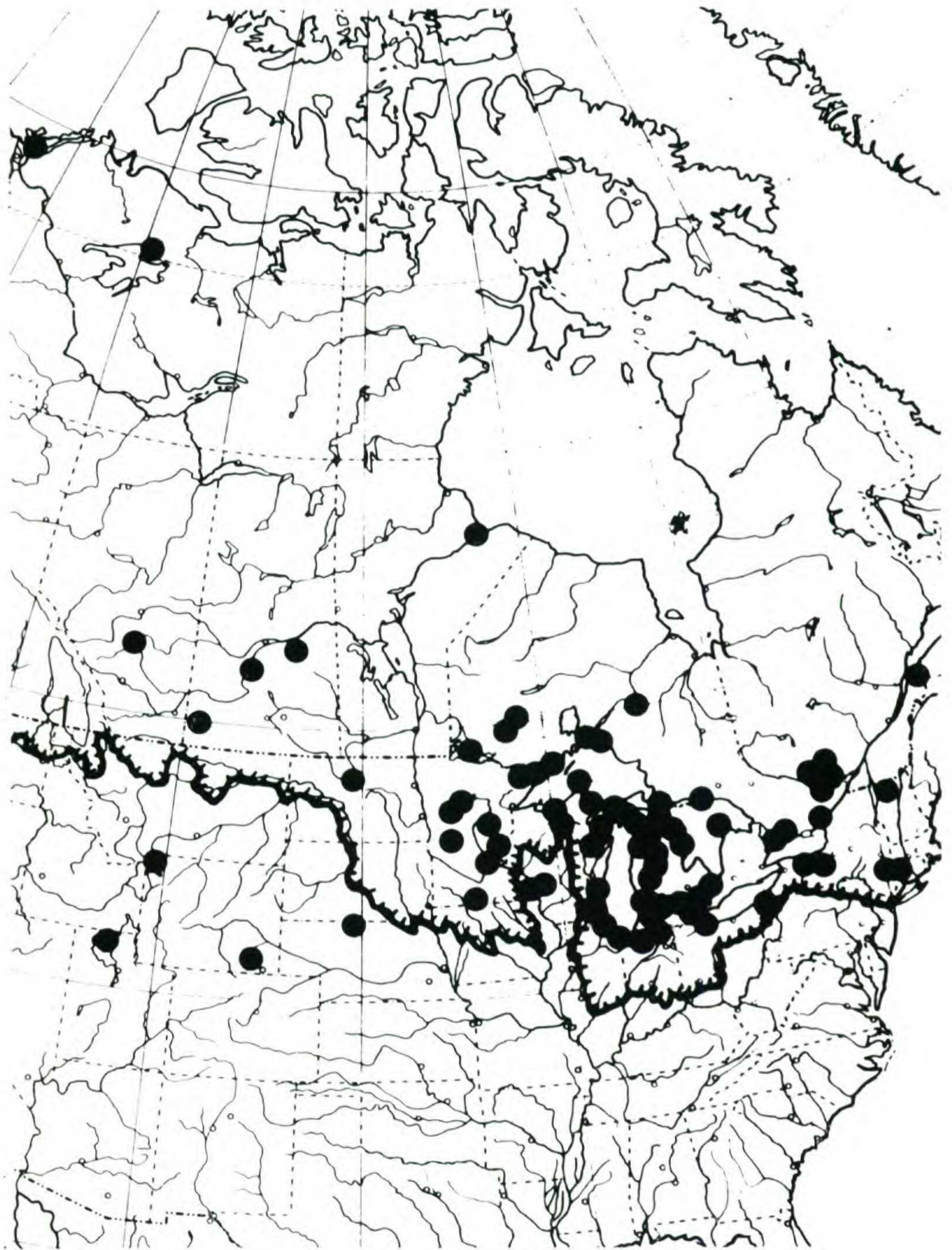


Fig. 4. Map of North America showing the documented distribution of *Potamogeton strictifolius*. The barred line represents the southern limit of Wisconsin Glaciation in the United States east and west of the Rocky Mountains (after Flint, 1957; Flint *et al.*, 1959).

For both species, I find, as does Voss (1972), that the usual number is five. If specimens are sterile and lacking winter buds and I must use vegetative characters, I then rely upon the apex shape and whether the leaves are revolute. In *P. strictifolius*, the apex is usually acute and the leaves are revolute. In *P. friesii*, the apex is obtuse to apiculate and the leaves are usually flat. However, as I indicated earlier and pointed by Voss (1972) one must use these characters with caution. In the late summer the margins of *P. friesii* roll under, thus the leaves become revolute.

REPRESENTATIVE SPECIMENS

CANADA: Alberta: Large pond, Lacombe, *Dixon* 691 (DAO, NY). Manitoba: York Factory, *Drummond* (GH). Northwest Territories: MACKENZIE DIST.: E branch of Mackenzie River, 68°40' to 68°55', Reindeer Station, *Porsild* 7234 (CAN). Ontario: THUNDER BAY DIST.: Black Fox Lake, *Haynes* 3750 (CAN, GH, LAF, MO, OS); Nipigon, Lake Superior, *Macoun* (CAN, NY, S). Quebec: GATINEAU CO.: Danford Lake, 45 mi. N of Ottawa, *Dore* 9032 (DAO, MO). Saskatchewan: Pike Lake, Saskatoon, *Fraser* 8 (DAO, GH). UNITED STATES: Connecticut: LITCHFIELD CO.: Indian Pond, Sharon, *Eames* 11868 (GH). Illinois: COOK CO.: Wolf Lake, Chicago, *Chase* 1709 (CGE, F, GH, ILL). Indiana: LAKE CO.: Lake George, East Chicago, *Hill* 144-1903 (GH, ILL, NY). Michigan: CHARLEVOIX CO.: Cunningham Lake, ca 6 mi SW of Iron-ton, *Voss & Haynes* 13602 (MICH). CHEBOYGAN CO.: Black River between its mouth and Alverno, *Haynes* 3379 (GH, MO, OS, US), *Haynes* 3384 (MO, OS, US), *Haynes* 3743 (GH, OS); Black Lake, near mouth of Upper Black River, *Haynes* 3777 (OS); Cheboygan River, *Haynes* 3798 (OS); Douglas Lake near source of Maple River, *Haynes* 3739 (GH, MICH, MO, NY, OS, UMBS, US). WAYNE CO.: Detroit River near Belle Isle, *Wheeler* (GH, ILL, NY, US). Minnesota: BECKER CO.: DeSota Lake, *Grant* 3269 (GH, NY, UC, US). Nebraska: CHERRY CO.: Willow Lake, *Thomson* 122 (US). New York: MONROE CO.: *Clausen & Hinkey* 4196 (GH, NY). North Dakota: MCHENRY CO.: Red Willow Lake, *Mabbott* 372 (US). Ohio: ERIE CO.: Sandusky Bay, *Pieters* (US). Pennsylvania: ERIE CO.: Presque Isle, *Garber* (GH). Utah: BOX ELDER CO.: Bear River, *Watson* 1136 (GH, K, NY, US). Vermont: CALEDONIA CO.: Sarah Moor Pond, 2 mi NW of Barnet, *Hotchkiss* 7804 (US). Wisconsin: WASHINGTON CO.: Big Cedar Lake, *Hotchkiss & Hoehler* 4264 (GH, US). Wyoming: ALBANY CO.: reservoir ca 6 mi. NE of Lookout, *Porter* 7370 (DAO, NY, UC, USP). PARK CO.: Firehole River S of Madison Junction, *Porter* 6385 (DAO, MO, NY, UC, UPS).

Potamogeton strictifolius × zosteriformis

Fernald (1932) named *Potamogeton longiligulatus* based upon flowering specimens from Newfoundland. The entity was said to resemble *P. hillii* by its bristle-tipped leaves but differed from the latter species by having numerous-nerved leaves. Voss (1967) reported that, at least in northern Michigan, the entity appeared to be a result of hybridization between *P. strictifolius* and *P. zosteriformis*, a species in the subsection *Compressi* of Hagstrom. Data gathered during my field studies in northern Michigan support Voss' conclusions. I have seen several instances where the putative hybrid was growing between populations of *P. zosteriformis* and *P. strictifolius*. The plants of the putative hybrid were morphologically intermediate between the two species. Therefore, until the putative hybrid can be studied in detail, I accept Voss' concept of the taxon.

SPECIMENS EXAMINED:

CANADA: Newfoundland: Straits of Belle Isle, pond in barrens S of Flower Cove, *Fernald & Long* 27330, (holotype, GH!; isotype, PH!, photo at DOA!). **Ontario:** BRUCE CO.: Bruce Peninsula, Stokes Bay, *Krotkov* 8627 (US). LAMBTON CO.: Sarnia Bay, *Dodge* (GH, photo at DAO). **UNITED STATES: Connecticut:** LITCHFIELD CO.: Salisbury, Twin Lakes, *Bissell* (GH). **Illinois:** LAKE CO.: Grayslake, *Dolbeare* 1444 (MICH). **Michigan:** CHEBOYGAN CO.: Black River between its mouth and Alverno, *Bedell & Prescott* 55 (UMBS), *Haynes* 3380 (GH, MO, OS, US), *Haynes* 3381 (GH, MO, OS, US), *Haynes* 3702 (OS), *Haynes* 3744 (OS), *Majors* (GH, NY, UMBS), *Voss* 11118 (GH), *Voss* 11359 (UMBS); Black Lake, bay at mouth of Black River, *Stuckey* 2411 (OS), *Stuckey* 3275 (OS, CAN), *Voss* 11745 (GH, NY), 11760 (UMBS); Cheboygan River, *Haynes* 3799 (OS). **ST. CLAIR CO.:** Algonac, Big Ditch, *Dodge* s.n. (US); Port Huron, *Dodge* s.n. (NY). **SCHOOLCRAFT CO.:** Lake McDonald, SE of Whitedale, *Uhler* 96 (US). **Minnesota:** BECKER CO.: Cotton Lake, *Hotchkiss* 6341 (GH). **HENNEPIN CO.:** Lake Minnetonka, *Keck & Stilwill* 416 (GH). **New York:** COLUMBIA CO.: Beebe Pond near Queechy Lake, *Haynes* 3344 (OS), *Haynes* 3801 (OS), *Smith & Ogden* 45590 (OS).

3. Potamogeton obtusifolius Mert. & Koch, in Röhling, Deutschland Flora 855. 1823. TYPE: (type not located), application of the name is from the illustration of *Potamo-*

geton gramineus auct. non L.: In Smith, English Bot. 11: pl. 2253. 1811.

Spirillus obtusifolius (Mert. & Köch in Röhling) Nieuwl. Amer. Midl. Naturalist 3: 19. 1913.

Potamogeton compressum var. *tenuius* Wahl. Flora Upsaliensis 60. 1820. TYPE: G. Wahlenberg, Upsala Sraklen, Ekebysja near Quam, 22 Aug. 1818, (holotype, UPS!).

Potamogeton obtusifolius var. *angustifolius* Fieber in Berchtold, Oekon.-tech. Flora Bohmens 275. 1838. TYPE: (not located).

Potamogeton obtusifolius var. *latifolius* Fieber in Berchtold, Oekon.-tech. Flora Bohmens 275. 1838. TYPE: (not located).

Stem green to green-brown, slightly compressed, usually without ridges, 35-90 cm long, 0.3-0.7 mm diam. Leaves light green to rufescent, usually flaccid, 3-nerved, 3.0-8.2 cm long, 1.0-3.5 mm wide; apex round to round apiculate; glands yellow-green to gold, 0.2-1.0 mm diam; lacunae of 1-3 rows each side of midrib; lateral nerves joining the midrib 0.2-1.2 mm from apex. Stipules usually white, slightly fibrous, rarely shredding at tip, convolute, 0.6-1.8 cm long, 0.5-1.2 mm diam. Winter buds abundant, terminal, 3.5-7.8 cm long, 2.3-5.1 mm wide; inner leaves undifferentiated; outer leaves 3-4 per side, apiculate to obtuse, without corrugations at base. Peduncles cylindrical, axillary, rarely recurved, 0.8-1.9 (-4.2) cm long, 0.5-1.0 mm wide. Spike cylindrical, 0.8-1.3 cm long, 4.6-7.0 mm wide; verticels 3, crowded or to 2.0 mm apart. Perianth segments 1.4-1.5 mm long, 1.1-1.3 mm wide. Fruit olive-green to brown, 2.5-3.6 mm long, 1.7-2.4 mm wide; keels absent or present, when present, ridged, to 0.2 mm high; beak mostly central, rarely forward, (0.2-) 0.6-0.7 mm long, 0.5-0.7 mm diam; sides rounded; wall texture smooth or rough. Chromosome number $2n = 26$ (Palmgren, 1939).

Distribution: Eastern Yukon to eastern Quebec, south to Washington, Wyoming, and New Jersey. Fruiting from early July to late September. Fig. 5.

Illustrations: Fernald (1932, pl. 14; 30, fig. 3; 34, fig. 4; 39, fig. 1).

In its winter buds, fruit, and peduncles, *Potamogeton obtusifolius* most closely resembles *P. hillii*. When in fruit, however, it can easily be separated from the latter species by its spikes being cylindric, whereas those of *P. hillii* are capitate. Sterile specimens of *P. obtusifolius* can usually be distinguished from *P. hillii* by the former having obtuse leaves and the latter having acute leaves. However, plants of *P. hillii* occasionally possess obtuse leaves.

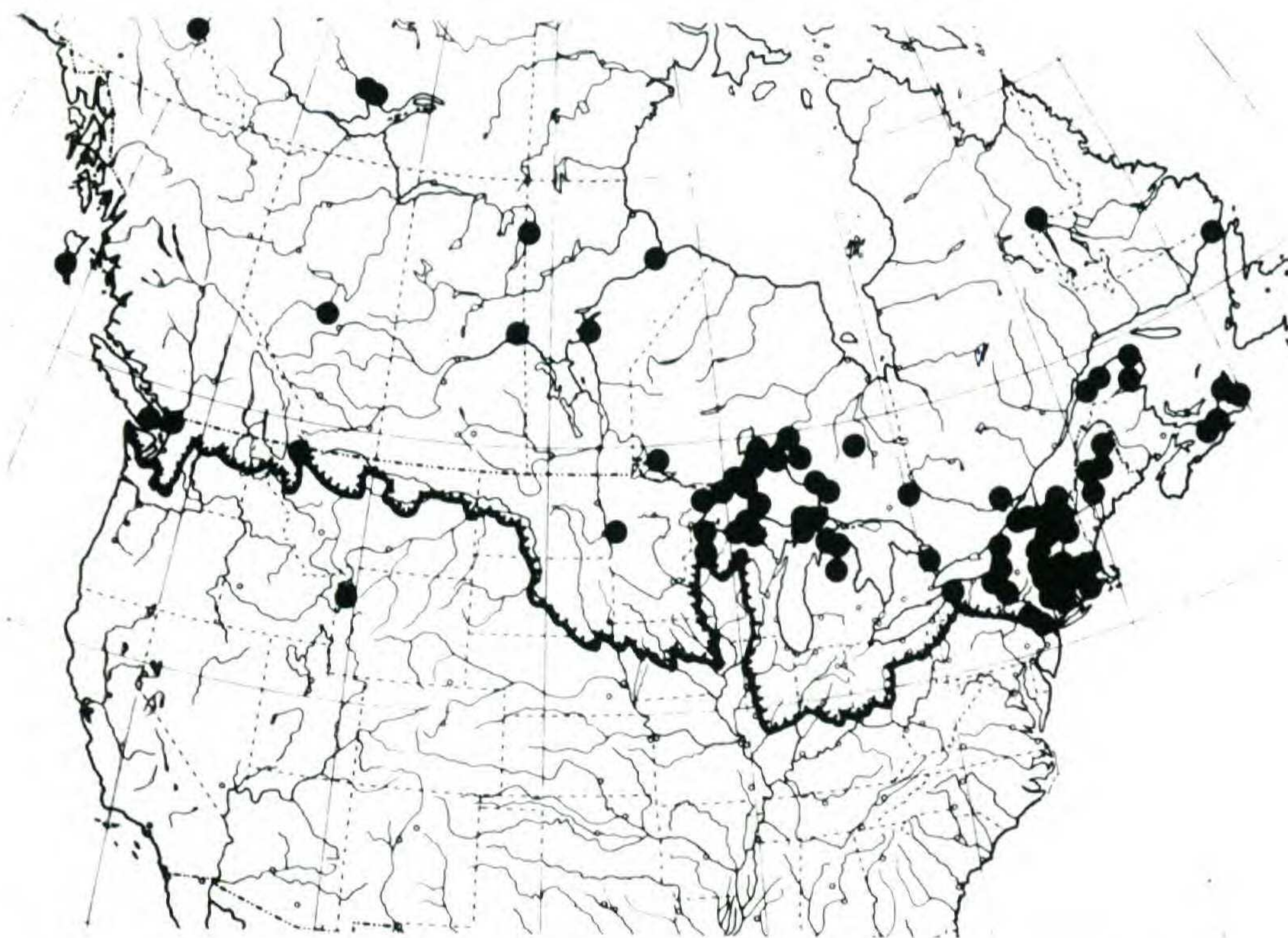


Fig. 5. Map of North America showing the documented distribution of *Potamogeton obtusifolius*. The barred line represents the southern limit of Wisconsin Glaciation in the United States east and west of the Rocky Mountains (after Flint, 1957; Flint *et al.*, 1959).

REPRESENTATIVE SPECIMENS

CANADA: Alberta: ca. 2 mi. W of Glenevis, *Moss* 12449 (CAN, DAO). **British Columbia:** VANCOUVER ISLAND: Cowichen, *Glendenmire* (CAN, GH). **Manitoba:** Fort Churchill, 58°67'N, 94°10'W, *Schofield & Crum* 6787 (CAN, F). **Northwest Territories:** MACKENZIE DIST.: small pool ca. 45.5 mi. WNW of Yellowknife, *Thieret & Reich* 7947

(F, OS, US). **Nova Scotia:** CAPE BRETON CO.: Mira Bay, *Macoun* 20755 (F, GH, CAN). **Ontario:** THUNDER BAY DIST.: Black Fox Lake, *Haynes* 3749 (CAN, GH, LAF, MO, OS, UC); Sibley Twp., Ravine Lake, *Taylor et al.* 232 (CAN, GH, UC). **Quebec:** Lake Memphremagog, Sargents Bay, *Churchill* (GH, K, MO). **GASPE CO.:** Riviere Bonaventure, *Marie-Victorin et al.* 33764 (F, GH, NY, PH). **Saskatchewan:** MACKENZIE DIST.: Meridian Creek near Amisk Lake, *Hudson* 1550 (DAO). **Yukon:** Sheldon Lake, Canol Road mi. 222, *Porsild & Breitung* 11511 (CAN). **UNITED STATES:** **Connecticut:** FAIRFIELD CO.: Norwalk River, Ridgefield, *Eames* 11717a (GH). **Maine:** PENOBSCOT CO.: Pushaw Stream, Old Town, *Ogden et al.* 1617 (CAN, GH, MO, NY, US). **PISCATAQUIS CO.:** cold clear stream, Foxcroft, *Fernald* 478 (GH, MO, US). **Massachusetts:** ESSEX CO.: ditch in Wenham, *Morong* (F, GH, ILL, PH); Pleasant Pond, Wenham, *Faxon* (GH, NY, US), *Ogden & Ogden* 1763 (CAN, DAO, F, GH, ILL, MICH, MO, NY, PH, UC, UPS, US). **Michigan:** KEWEENAW CO.: Beaver Pond, ca. 4 mi, S of Central Mine, *Robbins* (GH, MO, NY, PH). **LUCE CO.:** Bodie Lake, *Haynes* 3787 (OS). **SCHOOLCRAFT CO.:** Canoe Lake, *Haynes* 3741a (OS). **Minnesota:** ST. LOUIS CO.: West Two Rivers, Tower, *Hill* 218-1889 (CAN, ILL). **Montana:** GLACIER CO.: Howe Lake, Glacier National Park, *Hazzard* 480 (GH). **New Hampshire:** GRAFTON CO.: pond, Enfield, *Kennedy* (GH). **New Jersey:** MORRIS CO.: Rockaway River near Milton, *Williamson* (GH, PH). **New York:** ALBANY CO.: Alcove, *Shear* (GH, NY, UC). **Pennsylvania:** WAYNE CO.: Howell's Pond, *Twining* (GH, PH). **Rhode Island:** PROVIDENCE CO.: Fountain Spring Brook, Smithfield, *Lovewell* (GH). **Vermont:** ADDISON CO.: Little Otter Creek, Ferrisburg, *Eggleston & Grout* (F, GH, PH, US). **CALEDONIA CO.:** spring-fed pond, ca. 2 mi. N of Walden Village, *Haynes* 3829 (OS); Coles Pond, Walden Twp., *Haynes* 3837 (OS). **Washington:** SAN JUAN CO.: Summit Lake, Orcas Island, *Sutherland & Kern* 1182 (CAN, NY, UC). **Wisconsin:** ONEIDA CO.: stream, Three Lakes, *Hoffman* (GH, MO). **Wyoming:** TETON CO.: Beaver ponds near Moose, *Porter & Porter* 9405 (GH, UC).

4. **Potamogeton hillii** Morong, Bot. Gaz. (Crawfordsville) 6: 290. 1881. TYPE: *E. J. Hill*, Stagnant pools, Manistee, [Manistee Co.] Michigan, (holotype, NY!; isotypes, F[2 sheets]!, GH[2 sheets]!, ILL[4 sheets]!, K!, PH!).

Potamogeton porteri Fern. Mem. Amer. Acad. Arts 17: 73. 1932. TYPE: *T. C. Porter*, Run in Dillerville Swamp, near Lancaster, [Lancaster Co.] Pennsylvania, (lectotype, PH!; isoelectotypes, F[2 sheets]!, MO!, NY[2 sheets]!, PH[2 sheets]!).

Stems green to olive, slightly compressed, heavily ridged, 30-60 cm long, 0.5-1.0 mm diam. Leaves pale-green to olive-green, delicate, 3-nerved, 2.0-6.0 cm long, 0.6-2.5 (-4.0) mm wide; apex apiculate to bristle-tipped; glands present or absent, brown to green, 0.1-0.3 mm diam; lacunae of 1-2 rows each side of midrib; lateral nerves joining midrib (0.4-) 0.7-1.7 mm from apex. Stipules white to light brown, slightly fibrous, rarely shredding at tip, convolute, 7.0-16.0 mm long, 0.6-2.2 mm diam. Winter buds rare, terminal, 2.8-3.0 cm long, 1.5-3.0 mm wide; inner leaves undifferentiated; outer leaves 3-4 per side, acute to apiculate, without corrugations at base. Peduncles slightly clavate, axillary or terminal, rarely recurved, 6.0-13.5 mm long, 0.3-1.0 mm diam. Spike globose, (2.0-) 4.0-7.0 mm long, 4.6-7.0 mm diam; verticels 1-2, when 2, these crowded, 0.5-1.0 mm apart. Perianth segments 1.3-1.5 mm long, 1.1-1.5 mm wide. Fruit brown to light greenish-brown, dorsally and laterally keeled, 2.3-4.0 mm long, 2.0-3.2 mm wide; keels forming ridges, without undulations, to 0.2 mm high; beak central, rarely forward, 0.3-0.7 mm long, 0.2-0.6 mm diam; sides rounded rarely centrally depressed; wall texture rough. Chromosome number unknown.

Distribution: In cold stagnant or slow moving, often brown water, from northern Lower Peninsula Michigan to Vermont and south to northeastern Ohio and southeastern Pennsylvania. Fruiting from late June to late August. Fig. 6.

Illustrations: Fernald (1932, pl. 13; 30, fig. 2; 34, fig. 2).

In the original description, Morong cited only the following data: "excellent specimens obtained in August 1880, by Mr. Hill, at Manistee, Michigan . . ." He included no indication as to the location of the specimen. Hill prepared, from Manistee in August 1880, no less than 14 herbarium specimens on at least two separate days. Fernald (1932, p. 169), also giving no specimen location, designated as the type collection the one gathered by Hill on 10 August 1880.

However, in the collection at NY there is a specimen collected on 5 August 1880 by Hill and labeled in Thomas Morong's handwriting as "Type Specimen." Of the many other specimens examined by Morong, none of these others were indicated as types by Morong. Therefore, the 5 August specimen, having been designated by the author, then is the holotype and the one cited by Fernald then is a topotype.

Fernald (1932) named *Potamogeton porteri* based on several sheets collected by Thomas Porter in mill ponds near Lancaster, Pennsylvania. In the body of the original description Fernald did not cite any one specimen as the type. The data he gave are "PENNSYLVANIA: Cold streams or rivulets in Dillerville Swamp, Lancaster Co., October 5 and 6, 1860, Thos. C. Porter, distributed as *P. pusillus* and *P. obtusifolius* (TYPE in Herb. Acad. Sci. Nat. Phila.; duplicate in Herb. Gray; fragmentary (sterile) duplicates in Herb. Field Mus., Dudley, and Mo. Bot. Gard.)." In a footnote on the same page he states "Porter's labels, all of material collected on October 5, with the exception of one sheet marked October 6, indicate somewhat different habitats: 'Cold rivulets near Lancaster,' 'Near Lancaster,' 'In a rivulet, Dillerville swamp, Lancaster,' 'Stream in Dillerville Swamp, near Lancaster,' 'Run in Dillerville Swamp, near Lancaster.'"

I have seen the specimens at PH, GH, F, MO, and none of the sheets have the locality data given by Fernald in the body of the text. There are, in fact, three sheets at PH labeled by Fernald as *P. porteri*. He indicated "Type Collection" on two of these sheets, "Run in Dillerville Swamp, near Lancaster, Penn. October 5, 1860" and "Stream in Dillerville Swamp, near Lancaster, Penn. October 5, 1860." On the other sheet, "Cold rivulets near Lancaster, Pa. October 5," Fernald did not indicate "Type Collection." The two specimens labeled as "Type Collection" by Fernald are obviously the same taxon and both match the description. However, the one with data of "Stream in Dillerville Swamp, near Lancaster, Penn. October 5, 1860" is fertile

while the other is sterile. Hence, I am here designating the fertile one as the lectotype.

Fernald states (p. 74), "In its large fruit with prominent keel and recurved beak and its essential lack of glands at the base of the stipules *P. porteri* is close to *P. hillii*, but the latter species is wholly different in its acute, attenuate and thinner stipules; and in its attenuate almost bristle-tipped leaves with a single row of lacunae each side of the midrib and with the lateral nerves confluent with the midrib well below the tip." The specimens annotated by Fernald as *P. porteri* vary from ones with narrow leaves with apiculate leaf tips to very broad ones with obtuse leaf tips. The broad leaved specimens are quite distinct from characteristic *P. hillii*. However, the ones with the narrower leaves closely resemble *P. hillii* in all characters mentioned by Fernald. A locality of *P. hillii* in Cheboygan County, Michigan, first located by Dr. E. G. Voss in 1967, was visited by me during the summers of 1970, 1971, and 1972. I noticed a variability within the population from individuals with the characteristic narrow attenuate leaves with delicate stipules to ones with broad obtuse leaves with coarse stipules. Within this one population, a complete gradation exists from characteristic *P. hillii* to characteristic *P. porteri*. For this reason I believe *P. porteri* is a morphological extreme of *P. hillii*.

With the capitate inflorescence, short axillary peduncles, and fruits with a small dorsal keel, *Potamogeton hillii* closely resembles *P. foliosus*. However, it can be distinguished from the latter species by the large $2.3\text{--}4.0 \times 2.0\text{--}3.2$ mm fruits (the largest of any *Pusilli*), by the nearly bristle-tipped leaves and by the stipules being convolute. By the nearly bristle-tipped leaves, some individuals resemble *P. longiligulatus*, a proposed hybrid, but can be distinguished from this putative hybrid by the leaves having only 3 veins, whereas those of *P. longiligulatus* have mostly 7-9 veins. From all other *Pusilli*, *P. hillii* can be separated by its large fruits, short peduncles, and capitate inflorescences.

Fernald (1932) states that the *Pusilli* reproduce, for the most part, not by seeds, but by winter buds. He also states that winter buds are unknown in *Potamogeton hillii*. I have seen one sheet with well developed winter buds and several with ones that were immature. The winter buds, when present, with the inner leaves being unmodified, resemble small ones of *P. obtusifolius* in shape and structure, even in having the leaves round apiculate.

Potamogeton hillii has been considered to be extremely local throughout its range. This distribution is becoming more apparent with the destruction of the aquatic environment by pollution and dredging. In fact, Voss (1967) reported that the type locality of *P. hillii* has been destroyed.

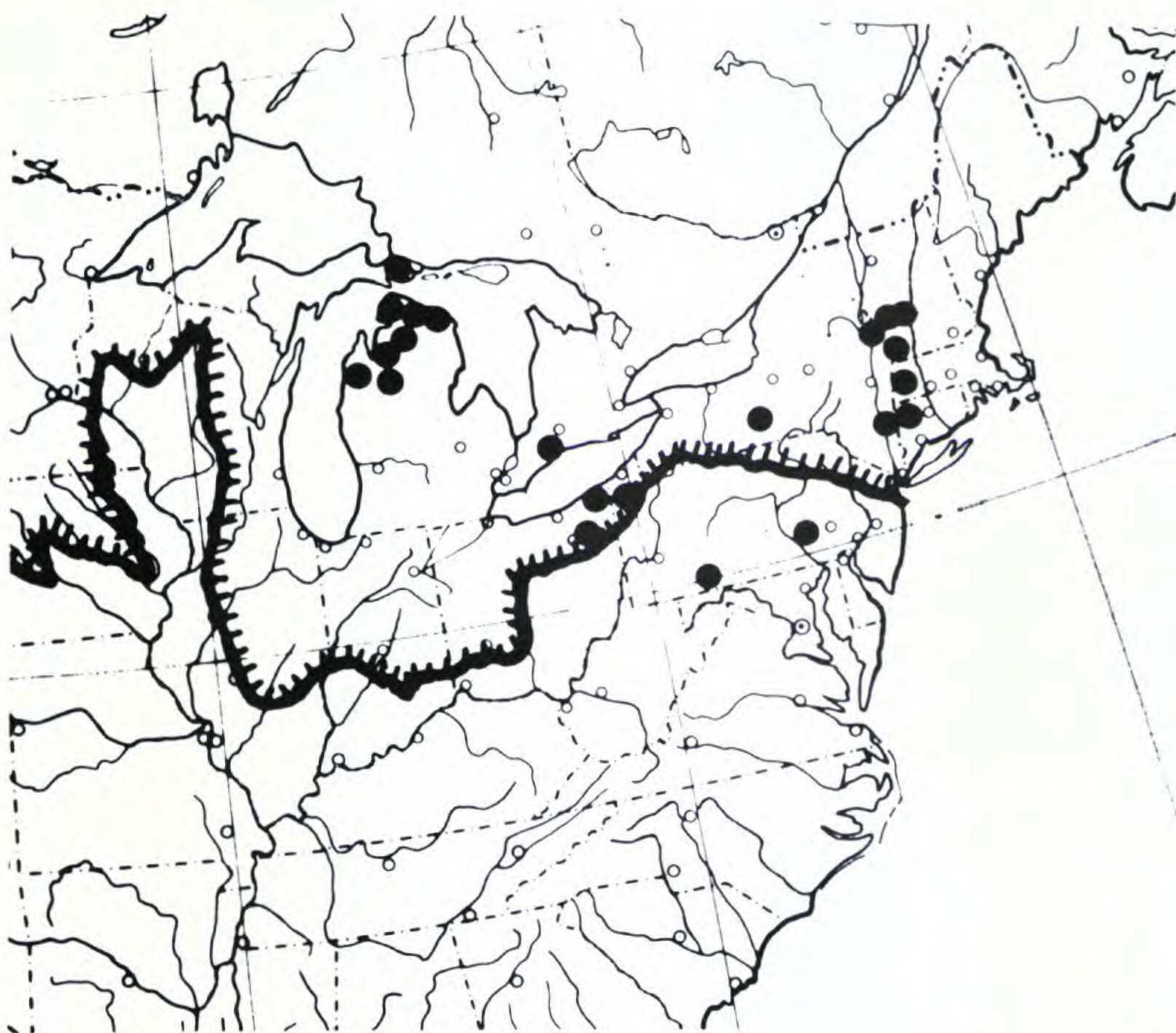


Fig. 6. Map of eastern North America showing the documented distribution of *Potamogeton hillii*. The barred line represents the southern limit of Wisconsin Glaciation (after Flint *et al.*, 1959).

Around 1900, the species was present in northeastern Ohio and northwestern Pennsylvania. This area has become heavily populated, with few if any natural areas remaining. The two Ohio counties, Portage and Ashtabula, have been rather heavily collected over the past 20 years. Some collectors thought they had collected the species, but after examining the specimens, I found them all to be *P. pusillus*. On the other hand, intensive field work in northern Michigan has shown the species to occur in no fewer than four localities within a radius of 30 miles of Cheboygan County. The same situation may prove to be true in other less heavily populated areas of its range, especially northeast New York state, as botanists continue to search for the species.

REPRESENTATIVE SPECIMENS

CANADA: Ontario: ELGIN CO.: near St. Thomas, *James* (DAO). **UNITED STATES: Connecticut:** LITCHFIELD CO.: Indian Pond, Sharon, *Eames* 11867 (GH). **Massachusetts:** BERKSHIRE CO.: pond fed by Karner Brook, South Egremont, *Weber* 1626 (CAN, F, GH, MICH, MO, NY, UC, US). **Michigan:** CHEBOYGAN CO.: Elliot Creek, 4 mi. E of Cheboygan, *Haynes* 3389 (GH, MO, OS, UC, US), *Haynes* 3713 (OS). EMMET CO.: Cecil Bay marsh, 4 mi. SW of Mackinaw City, *Voss* 14061 (CAN, GH, MICH, MSC, NY, OS, UMBS, WIS). MAC-KINAC CO.: small stream ca. 1 mi. S of Engadine, *Haynes* 4025 (ASC, DAO, F, FSU, GH, K, MICH, MO, MSC, NY, OS, PH, SMU, TENN, TEX, UC, US, VDB, WIS, WVA). MANISTEE CO.: Manistee, *Morong* (GH, MICH, NY, US). OTSEGO CO.: outlet of Grass Lake, *Stuckey* 1300 (GH, MICH, NY, OS, UMBS). PRESQUE ISLE CO.: mouth of Black Mallard River, *Haynes* 3390 (F, GH, MO, NY, OS, PH, UC, US), *Haynes* 3714 (OS), *Haynes* 3740 (ASU, GH, LAF, MO, NY, OS, PH, QFA, UC, VDB, US), *Haynes* 3890 (OS). **New York:** THOMPCKINS CO.: Ithaca, Lake Cayuga, *Dudley* (CAN, F, GH, MICH, MO, US). WASHINGTON CO.: creek 2 mi. N of Dresden Station road, *Haynes* 3342 (GH, MICH, MO, OS, UC, US). **Ohio:** ASHTABULA CO.: pools, Ashtabula, *Hill* (F, ILL). **Pennsylvania:** BEDFORD CO.: millpond S of Woodbury, *Hotchkiss* 6003 (GH, US). **Vermont:** WINDSOR CO.: Evarts Pond, Windsor, *Dudley* (GH, NY, UC, US).

5. *Potamogeton foliosus* Raf., Med. Repos. Hexade 2, 5: 354. 1808.

Stems green to olive, slightly compressed and ridged, 4-75 cm long, 0.2-1.2 mm diam. Leaves pale green to olive,

rarely rufescent, delicate, 1-3 (-5)-nerved, 1.3-8.2 cm long, 0.3-2.3 mm wide; apex acute to apiculate, rarely with a bristle; glands present or absent, black to gold, to 0.5 mm diam; lacunae absent or to 2 rows each side of midrib; lateral nerves joining the midrib 0.5-1.2 mm below the apex. Stipules greenish to brown, rarely white, delicate to fibrous, shredding or not at the tip, connate or convolute, 0.2-2.2 cm long, 0.2-1.7 mm diam. Winter buds uncommon, lateral or terminal, 0.9-2.5 cm long, 0.6-2.0 mm wide; inner leaves rolled into a hardened fusiform structure; outer leaves 1-3 per side, acute to apiculate, without corrugations at base. Peduncles clavate, mostly in axiles of lower, rarely upper, leaves, usually recurved, 0.3-1.1 (-3.7) cm long, 0.3-1.4 mm diam. Spikes capitate to cylindric, 1.5-7.0 mm long, 1.0-6.0 mm diam; verticels 1-2, when 2, these usually crowded, 0.6-1.2 (-2.0) mm apart. Perianth segments 0.4-1.4 mm long, 0.3-1.0 mm wide. Fruit pale green to olive or brown, dorsally keeled, 1.4-2.7 mm long, 1.1-2.2 mm wide; keel undulate winglike, to 0.4 mm high; beak central, rarely forward, 0.2-0.6 mm long, 0.1-0.4 mm diam; sides rounded to centrally depressed; wall texture smooth.

Potamogeton foliosus is most similar to *P. hillii* in its short clavate peduncles and capitate inflorescence. However, when in fruit, *P. foliosus* can be separated from the latter species by the presence of a dorsal undulate wing on the fruit. The fruit of *P. hillii*, on the other hand, is three-keeled — two lateral and one dorsal ridge which does not appear as a thin undulating wing. Vegetatively, *P. foliosus* is most similar to *P. pusillus*. From *P. pusillus* var. *tenuissimus*, *P. foliosus* often can be distinguished by the near lack of lacunae. From *P. pusillus* var. *pusillus*, however, the separation is not that simple. Fernald (1932) suggests that *P. foliosus* may be separated from *P. panormitanus* [var. *pusillus*] by the absence of nodal glands. Voss (1972), on the other hand, has questioned this character as reliable. In most fruiting specimens of *P. pusillus* [var. *pusillus*] from Michigan, Voss could not find evident nodal glands. Data gathered by me from examination of

hundreds of herbarium specimens and many populations in the field support Voss's conclusions. Therefore, I give little value to the absence of glands as a character for separating these two taxa. Although intermediates occur, the only character which I have been able to consider with any reliance is the coarseness of the stipular veins. Those of *P. foliosus*, for example, are usually evident, appearing as ridges extending the length of the stipules. The veins are not usually so evident in *P. pusillus*.

5a. **Potamogeton foliosus** var. **foliosus**

P. foliorum Raf., Med. Repos. Hexade 3, 2: 409. 1811. (orthographic variant). *P. pauciflorus* Pursh, Flora Amer. Sept. 121. 1814. *P. foliosus* Raf. var. *genuinus* Fern., Mem. Amer. Acad. Arts 17: 43. 1932. TYPE: *Michaux*, in rivis affluente mari inundatis Carolinae inferioris [South Carolina] (holotype, P; photograph of holotype, GH!).

Potamogeton niagarensis Tuckerm., Amer. J. Sci. Arts Series 2, 7: 354. 1849. *P. pauciflorus* Pursh var. *niagarensis* (Tuckerm.) Robbins in Gray, Man. Bot. North. U. S., ed. 2. 435. 1856. *P. foliosus* Raf. var. *niagarensis* (Tuckerm.) Morong, Mem. Torrey Bot. Club 3: 39. 1895. *Spirillus foliosus* (Raf.) Nieuwl. var. *niagarensis* (Tuckerm.) Nieuwl., Amer. Midl. Naturalist 3: 18. 1913. *P. foliosus* Raf. f. *niagarensis* (Tuckerm.) Hagstrom. Kongl. Svenska Vetenskapsakad. Handl. 55(5): 91. 1916. TYPE: *Tuckerman*, Hogback, Niagara Falls, [Niagara Co.] New York, (holotype, NY!; isotypes, GH!, K!).

Potamogeton pauciflorus Pursh var. *californicus* Morong, Bot. Gaz. (Crawfordsville) 10: 254. 1885. *P. foliosus* Raf. var. *californicus* (Morong) Morong, Mem. Torrey Bot. Club 3: 40. 1895. *P. californicus* (Morong) Piper, Contr. U.S. Natl. Herb. 11: 98. 1906. *P. foliosus* Raf. f. *californicus* (Morong) Hagstrom, Kongl. Svenska Vetenskapsakad. Handl. 55(5): 91. 1916. TYPE: *S. B. & W. F. Parish* 940, submerged aquatic, streams, San Bernardino, San Bernardino Co., California, (holotype, NY!; isotypes GH!, MO!, PH!).

Potamogeton foliosus Raf. var. *macellus* Fern., Mem. Amer. Acad. Arts 17: 46. 1932. TYPE: *E. & C. E. Faxon* Fresh Pond, Cambridge, [Suffolk Co.] Massachusetts, (holotype, GH; isotype, US!).

Stems 4-72 cm long, 0.2-1.2 mm diam. Leaves 1-3 (-5)-nerved, 1.3-8.2 cm long, 0.3-2.3 mm wide; apex acute to apiculate, rarely with a bristle; glands rare, to 0.3 diam; lacunae absent or to 2 rows each side of midrib; lateral nerves joining the midrib 0.5-1.2 mm below the apex. Stipules greenish to brown, delicate to slightly fibrous, rarely shredding at the apex, connate, 0.2-2.2 cm long, 0.2-1.7 mm diam. Winter buds lateral, 0.9-1.8 cm long, 0.6-1.0 mm wide. Peduncles usually clavate, recurved, 0.3-1.1 (-3.7) cm long, 0.3-1.4 mm diam. Spikes usually capitate, rarely cylindric, 1.5-7.0 mm long, 1.0-6.0 mm diam; verticels 1-2, when 2, these crowded, 0.6-1.2 (-2.0) mm apart. Perianth segments 0.4-1.4 mm long, 0.5-1.0 mm wide. Fruit olive to green-brown, 1.5-2.7 mm long, 1.2-2.2 mm wide; keel 0.1-0.4 mm high; beak 0.2-0.6 mm long, 0.2-0.4 mm diam. Chromosome number, $2n = 28$ (Stern, 1961).

Distribution: Widespread, in waters of lakes, springs, streams and rivers, from central Alaska to Nova Scotia and south to southern Guatemala and Jamaica. Fruiting from late May to late October. Fig. 8.

Illustrations: Fernald (1932, pl. 3; 29, fig. 1; 32, fig. 3; 38, fig. 1).

Potamogeton foliosus was first recognized by Michaux (1803) when he reported *P. gramineus*? L. for North America. Rafinesque (1808), noticing that many of the Western Hemisphere plants represented different species from those of Europe, listed several species of Michaux which he later intended to describe. Among these was "*P. gramineum* to be described later as *P. foliosum*." Indeed, he did later describe the taxon (Rafinesque, 1811), but it was spelled as *P. foliorum* rather than as *P. foliosum*. However, the name of *P. foliosum* [*foliosus*] was validly and effectively published in 1808 when he made direct ref-

erence to the published description of *P. gramineum* of Michaux.

Pursh (1814) applied a superfluous name — *Potamogeton pauciflorus* — to Michaux's specimen. Other botanists either overlooked or neglected Rafinesque's name and accepted instead the one of Pursh. Tuckerman (1849) recognized that two forms — a large-leaved form and a small-leaved form — of *P. pauciflorus* Pursh [*foliosus*] existed. He divided the group into two species, applying *P. niagarensis* Tuckerm. to the larger-leaved individuals and retaining the name *P. pauciflorus* for the smaller-leaved ones. After noticing considerable morphological integration, Fernald (1932) chose to consider the two taxa at the varietal rank. After having examined Michaux's specimen at Paris, Fernald determined the specimen to be the large-leaved entity. Thus, *P. foliosus* and *P. pauciflorus* actually applied

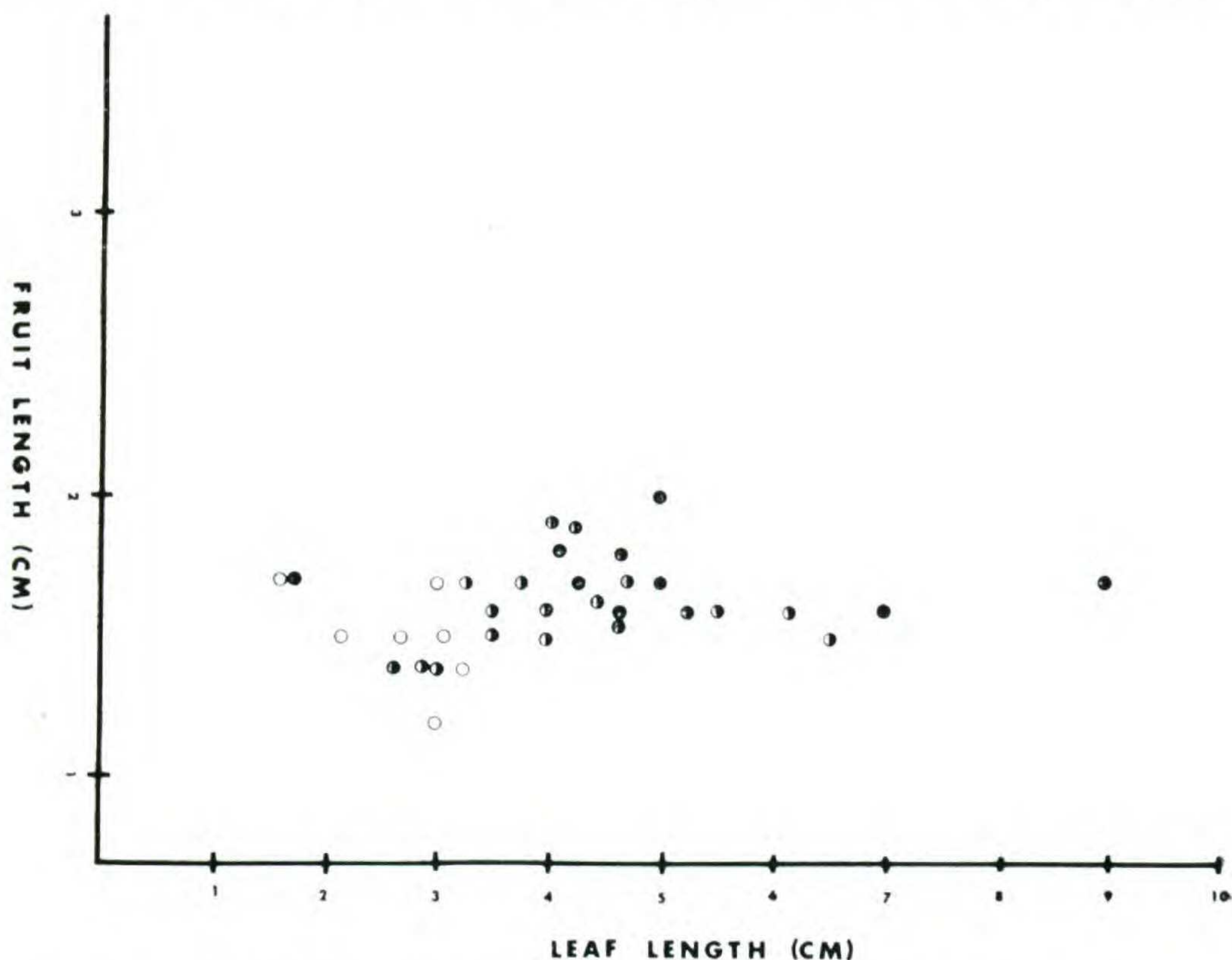


Fig. 7. *Potamogeton foliosus* var. *foliosus*. Scatter diagram comparing leaf length, fruit length, and number of nerves per leaf. 1 nerve, open circle; 3 nerves, half-closed circle; 5 nerves, dot.

to this growth form. Therefore, the smaller-leaved plants were unnamed. Fernald then named the smaller-leaved specimens *P. foliosus* var. *macellus* Fern. and called the larger river form var. *genuinus* [now correctly as var. *foliosus*]. I have examined thousands of specimens in the field and herbarium. Many of these have been plotted on scatter diagrams (see Fig. 7). Although only three char-

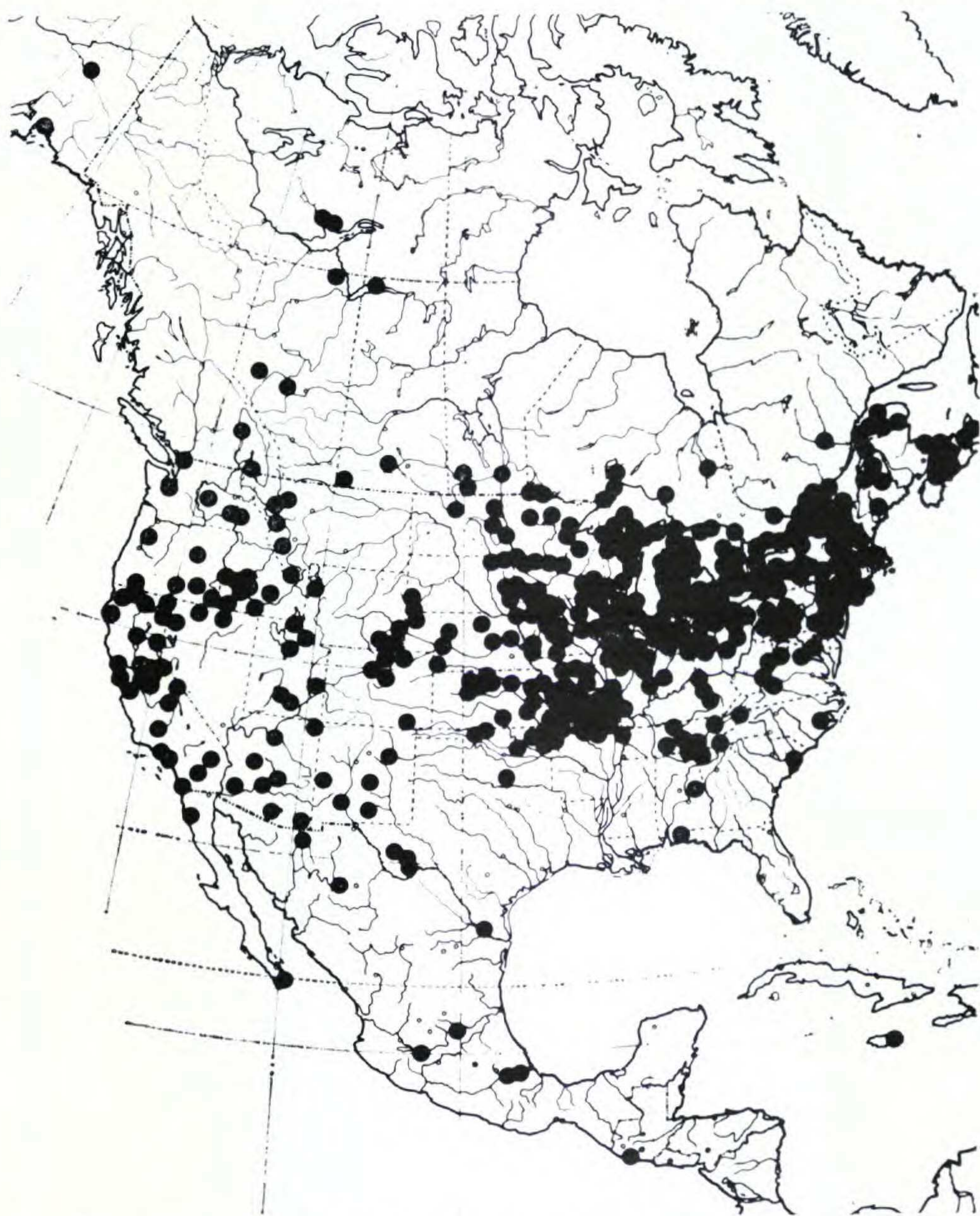


Fig. 8. Map of North America showing documented distribution of *Potamogeton foliosus* var. *foliosus*.

acters are used here, other characters were plotted and similar patterns developed. Data gathered from these studies indicate that a continuous gradient exists from ones with the largest leaves to those with the smallest leaves. The two groups do not appear to be separated into distinct geographical areas, with the intermediates in areas of overlap. Instead, these data indicate that the larger-leaved individuals occur in rapidly flowing waters, the intermediates occur in slow moving streams, and the smaller-leaved plants occur in lakes or ponds. Sculthorpe (1967) indicates that the size and shape of the leaves of many species of *Potamogeton* vary greatly with different rates of water flow. This is probably the situation with *P. foliosus*. I am, thus, considering var. *macellus* to be an ecological growth form of *P. foliosus*, and therefore, am not formally recognizing it.

REPRESENTATIVE SPECIMENS

CANADA: **Alberta:** Wood Buffalo Park, *Raup* 1562 (CAN, NY, UC). **British Columbia:** Revelstoke, *Macoun* 3037 (CAN, NY). **Manitoba:** Little Saskatchewan, Rapid City, *Macoun* 16482 (CAN, GH). **Northwest Territories:** small lake, 38.3 mi. WNW of Yellowknife, *Thieret & Reich* 8356 (F, OS). **Nova Scotia:** KINGS CO.: Canard River, *Smith et al.* 11446 (CAN, DAO). **Ontario:** FRONTENAC CO.: Kingston, Smith Falls, *Fowler* (CGE, MO, US). **Prince Edward Island:** QUEENS CO.: ponds, Southport, *Fernald & St. John* 6782 (CAN, K, NY, US). **Quebec:** NEW-RICHMOND CO.: Bonaventure River, *Marie-Victorin et al.* 33839 (CAN, F, MU, NY, PH). **Saskatchewan:** MOOSE JAW DIST.: Mortlach, *Hudson* 1143 (DAO). **GUATEMALA:** **Dept. Esquintla:** mountain stream, Finca San Filipe, *Muenschner* 12074 (GH, OS). **JAMAICA:** **Portland:** Rio Grande, *Maxon & Killip* 265 (ILL). **MEXICO:** **Baja California:** Rancho San Jacinto, 45 mi. S. of Eusenada, *Wiggins & Demaree* 4749 (F, MICH, MU, NY, US); stream, Santiago, *Wiggins* 5662 (MICH, NY, UC, US). **Chihuahua:** DEPT. DE GUERRERO: stream near Minaca, *Shreve* 7993 (F, GH). **Guanajuato:** DEPT. ATOTONILCO: just S of village of Santuario, between San Miguel Allenda and Dolores Hidalgo, *Ogden* 51149 (OS). **Michoacan:** Rio Duero at Zamora, *Ogden* 51183 (OS). **Puebla:** DIST. DE TEPEACA: San Hipalito, vicinity of Puebla, *Arsene* 2360 (ILL, NY, US). **Sonora:** Fronteras, *Hartman* 992 (GH, NY). **Veracruz:** Orizaba, Engenio, Rio Blenio, *Muller* 1330 (NY). **UNITED STATES:** **Alabama:** JACKSON CO.: Paint Rock River, Larkin Fork, *Harper* 2998 (GH, MO, NY,

PH, US). **Alaska:** 2 mi. SW of College, small pond, *Smith* 1911 (CAN). **Arizona:** Colorado Havasupai Canyon, *Clover* 5218a (MICH, US). **Arkansas:** FULTON CO.: Mammoth Springs, Spring River, *Thomas & Smith* 17094 (OS). **California:** LOS ANGELES CO.: Lancaster, *Elmer* 3504 (GH, K, NY, UC, US). SISKIYOU CO.: near Mt. Shasta, Abrams Lake, *Heller* 13908 (F, ILL, MO, NY, PH, UC, US). **Colorado:** DENVER CO.: Denver, Platte River, *Jones* 600 (F, NY, US). **Connecticut:** LITCHFIELD CO.: Litchfield-Morris Wildlife Sanctuary, Bantam Lake, *Dwyer* 2150 (NY). **Delaware:** NEW CASTLE CO.: near Wilmington, Brandywine Creek, *Commons* (PH). **District of Columbia:** Washington, *Ward* (GH, UPS). **Georgia:** CHATTOOGA CO.: 2.8 mi. E 30°N of Trion, small pond below Greeson Springs, *Duncan & Harris* 12842 (GH, LAF, MICH, US). **Idaho:** BOISE CO.: 20 mi. S of Idaho City, marsh, *Hitchcock & Muhlick* 9947 (NY, UC). **Illinois:** COOK CO.: Englewood, ditches, *Hill* (F, GH, ILL, US). ST. CLAIR CO.: East St. Louis, *Eggert* (CAN, F, ILL, K, MICH, NY, PH, OS, US). STARK CO.: near Wady Petra, prairie pond, *Chase* 1148 (ILL, MO, NY, PH). **Indiana:** LAKE CO.: Wolf Lake, West Bay, *Chase* 1461 (F, ILL, MO, PH, US). **Iowa:** CLAY CO.: Lake Twp, Dan Greene's slough, N end, *Hayden* 820 (MO, NY, PH, US). EMMET CO.: Estherville, running water, *Cratty* (GH, ILL, MO, NY, US). PALO ALTO CO.: Highland Twp, 2 mi. S of Ruthven, Virgin Lake, *Hayden* 10125 (MO, NY, PH, US). **Kansas:** RILEY CO.: ponds, *Pond* 1100 (MICH, MO, NY, US). **Kentucky:** FAYETTE CO.: near Lexington, brook, *Peter* (K, MICH, NY, PH). **Maine:** PISCATAQUIS CO.: Dover, river margin, *Fernald* 479 (MO, US). **Massachusetts:** MIDDLESEX CO.: Cambridge, Fresh Pond, *Morong* (F, MO). **Michigan:** CHEBOYGAN CO.: Douglas Lake, Marl Bay, *Haynes* 3923 (OS). EMMET CO.: small arm of Carp Lake, *Haynes* 3374 (GH, OS, UC, US), *Haynes* 3705 (ILL, OS), *Haynes* 3745 (OS), *Haynes* 3888 (OS). **Minnesota:** CLEARWATER CO.: Bohal Lake, *Grant & Oosting* 3228 (NY, UC, US). **Missouri:** BARRY CO.: Eagle Rock, river, *Bush* 511 (CGE, GH, MO, US). BUTLER CO.: Poplar Bluff, *Eggert* (CAN, F, K, MO, OS, US). OREGON CO.: Thomasville, spring pond, *Steyermack & Palmer* 41701 (MO, NY, PH, US). **TEXAS:** SW of Plato, Roubidoux Creek, *Steyermack* 25006 (DAO, F, NY, OS). **Montana:** MISSOULA CO.: ca. 6 mi. E of Lolo Hot Springs, small slough, *Hitchcock* 23978 (DAO, ILL, NY, US). **Nebraska:** LINCOLN CO.: North Platte, slough, *Shear* 4445 (GH, NY, US). **New Hampshire:** GRAFTON CO.: Hanover, Count River, *Jesup* (MO). **New Jersey:** MORRIS CO.: Oak Ridge, running water, *Mackenzie* 3736 (MO, NY, US). **New Mexico:** LINCOLN CO.: Bonita River, ca. 6½ mi. NW of Alto, *Haynes* 2923 (LAF). **New York:** COLUMBIA CO.: 1¼ mi. SSW of West Copake, Lower Rhoda Pond, *Haynes* 3802 (OS). DUTCHESS CO.: 1½ mi. SW of Pine Plains, Stissing Pond, *Haynes* 3804 (OS). ESSEX CO.: near Ticonderoga, outlet of Lake George, *Haynes* 3333 (OS), *Haynes* 3336 (OS). NIAGARA CO.:

Niagara Falls, mill race near Cataract House, *Hill* 26-1887 (ILL, MICH, MO). PUTNAM CO.: Carmel, Glendia Lake, *Muenschner & Curtis* 5447 (MO, NY, PH, UC, US). WARREN CO.: Lake Luzerne boat launch, *Haynes* 3814 (OS). **Nevada:** ELKO CO.: Copper Mountains, 3 mi. S of Coon Creek Pass, *Maguire & Holmgren* 22411 (CAN, NY, US). **North Carolina:** CHEROKEE CO.: N of Marble, limestone quarry, *Radford* 4812 (NY). **North Dakota:** CASS CO.: Fargo, ditch, *Stevens* 1376 (CAN, UC, US). **Ohio:** AUGLAIZE CO.: Lake St. Marys Fish Hatchery, *Haynes* 3427 (GH, MICH, OS, US); 2 mi. SE of Wapakoneta, borrow pit, *Haynes* 3420 (OS, US). CHAMPAIGN CO.: Kaiser Lake State Park, *Haynes* 3435 (MICH, OS, UC, US). ERIE CO.: 4 mi. NW of Castalia, *Haynes* 3247 (MICH). LOGAN CO.: 1.9 mi. due ESE of Russells Point, *Haynes* 3415 (MICH, OS, PH, US). OTTAWA CO.: Lake Erie, North Bass Island, Fox's Marsh, *Haynes* 3145 (OS). PORTAGE CO.: 5½ mi. NW of Ravenna, borrow pit, *Haynes* 3452 (GH, MICH, MO, OS, US). **Oklahoma:** OTTAWA CO.: Hattenville, overflow pond, *Stevens* 2481 (GH, ILL, K, MO, NY, US). WOODS CO.: Waynoka pond, *Stevens* 1768 (GH, ILL, K, MO). **Oregon:** pond on the Willamette River, *Hall* 492 (F, GH, ILL, MO, NY, US). **Pennsylvania:** BERKS CO.: 1 mi. SE of Pine Forge, Manatawny Creek, *Wilkins* 5619 (GH, PH). **South Carolina:** GEORGETOWN CO.: Georgetown, Hobcaw Plantation, *Alexander* 148 (US). **South Dakota:** PENNINGTON CO.: Sheridan Lake, *Porter* 6593 (DAO, UPS). **Tennessee:** FRANKLIN CO.: Sherwood, *Eggert* (GH, MO, US). **Texas:** JEFF DAVIS CO.: Limpia Canyon, *Tracy* 288 (GH, NY). **Utah:** CACHE CO.: Bear River Range, E side of Tony Grove Lake, *Maguire & Snell* 16048 (DAO, ILL, MICH, NY). GRAND CO.: Hill Creek near Weaver Reservoir, *Holmgren et al.* 2358 (DAO, ILL, NY, UPS). **Vermont:** ORLEANS CO.: ca. 1 mi. W of Craftsbury Common, backwater of Black River, *Haynes* 3839 (OS); 1 mi. S of Craftsbury Common, backwater of Black River, *Haynes* 3840 (OS). WINDSOR CO.: Plymouth, *Eggleston* (F, MO, PH, US). **Virginia:** BOTETOURT CO.: Cloverdale, Tinker Creek, *Wood* 6133 (GH). **Washington:** GRANT CO.: Pond SW of Moses Lake, *St. John et al.* 4960 (MO, UC). **West Virginia:** GREENBRIAR CO.: Dunlap Creek, *Berkley* 1194 (MO). **Wisconsin:** WAUSHARA CO.: Poy Sippi, Pine River, *Hill* (CAN, F, GH, ILL). **Wyoming:** LARAMIE CO.: Laramie Mountains, Middle Fork of Crow Creek, *Porter* 6320 (DAO, MO, NY, UPS).

5b. **Potamogeton foliosus** var. **fibrillosus** (Fern.) Haynes & Reveal, *Rhodora* 75: 76. 1973.

Potamogeton fibrillosus Fern. Mem. Amer. Acad. Arts 17: 51. 1932. TYPE: W. C. Cusick 2598, in warm spring, margin of Harney Valley, "P" Ranch, [Harney Co.] Oregon, (holotype, GH!; isotypes, F! K!, MO!, NY!, UC!, US!).

Stems 20-75 cm long, 0.3-1.2 mm diam. Leaves (1-) 3-nerved, 2.1-5.5 mm long, 0.5-1.7 mm wide; apex acute apiculate; glands usually present, black to gold, to 0.5 mm diam; lacunae absent; lateral nerves joining midrib 0.6-0.8 mm below apex. Stipules brown, rarely white, fibrous, shredding at tip, often convolute, 0.4-12.1 cm long, 0.5-1.2 mm diam. Winter buds lateral or terminal, 1.2-2.5 cm long, 0.8-2.0 mm wide. Peduncles clavate, recurved, 6.5-9.2 (-22.0) mm long, 0.4-1.0 mm diam. Spike capitate to cylindric, 1.7-5.5 mm long, 1.0-4.0 mm diam; verticels 1-2, when 2, then 0.6-0.8 mm apart. Perianth segments 0.5-0.7 mm long, 1.1-1.2 mm wide. Fruit pale-green, 1.4-1.7 mm long, 1.1-1.2 mm wide; keel to 0.2 mm high; beak ca. 0.2 mm long, 0.1-0.2 mm wide. Chromosome number unknown.

Distribution: In waters, often warm, of shallow lakes, springs, streams and rivers, from southwestern Washington southward through southeastern Oregon, hence eastward to southeastern Wyoming. Fruiting from mid-June to mid-September. Figure 9.

Illustrations: Fernald (1932, pl. 5; 28, Fig. 5; 32, Fig. 5).

In 1932, Fernald proposed *Potamogeton fibrillosus* based on specimens collected in Wyoming, Idaho, Oregon and Washington. He noted that the new species closely resembled *P. foliosus* Raf. in its foliage, peduncles and small dorsally keeled fruits. Fernald said that *P. fibrillosus* differed from *P. foliosus* by its stipules which disintegrate into "rope-like" fibers and are thus open or convolute, and by having fruits with a less developed keel and more nearly median beak. Fernald (1932, p. 52) stated his reservations in assigning specific rank to this new entity: "The plant will doubtless be found to have a broader range, when it may prove to be a marked geographic variety of the widespread *P. foliosus*."

Several collections, especially from Yellowstone National Park of Wyoming and from southeastern Oregon, are distinct from *Potamogeton foliosus*. In general, these speci-

mens differ from *P. foliosus* not only in having the stipules disintegrating into fibers and fruits with poorly developed keels, but also in having cylindric, interrupted inflorescences and leaves with basal glands — the last two characters not mentioned by Fernald, but are present even on the holotype.

Other collections from the Yellowstone region are not so distinct. One such collection (*Haynes 3849*) has fruits, including the keel, which are identical with those of *Potamogeton foliosus*, but the inflorescence is capitate and the stipules only rarely disintegrate into fibers. Yet, basal glands are present. Flowering specimens from Albany County, Wyoming, taken by C. L. Porter (*3473*) are similar to *P. fibrillosus* in having basal glands and short, clavate peduncles. However, in this collection, the stipules only rarely disintegrate into fibers. Flowering specimens obtained by Maguire (*21578*) in northern Utah commonly produce fibers when the stipules decay, but basal glands are rarely found.

Hitchcock (1969) regarded *Potamogeton fibrillosus* as a distinct species, but conceded its close relationship with *P. foliosus*. Porter (1963) reduced *P. fibrillosus* to synonymy, regarding it only as a local form of *P. foliosus* produced by the rather warm-water conditions of "geyser formations and hot springs" in the Yellowstone area. Porter stated (1963, p. 9) "The warm water hastens disintegrations of the sheaths by bacterial action." This is not always the case, however, in northern Utah or southeastern Oregon where the water is often cool. Here the stipules still form fibers. In the same general region, *P. foliosus* is known to occur in similar environmental conditions and at approximately the same degree of development. Therefore, the possibility that mere bacterial activity (or some other type of mechanical breakdown) being the only cause of the fibrous stipules seems unlikely. For this reason and that the extremes can be distinguished quite easily, Haynes and Reveal (1973) thought that *P. fibrillosus* should be taxonomically recognized. However, since many intermediate

forms can be found, they could not justify the specific rank and therefore ranked the taxon at the varietal level.

From var. *foliosus*, the var. *fibrillosus* may be distinguished by its poorly developed keel, cylindric and interrupted inflorescence, fibrous stipules and glands present at the base of most leaves.

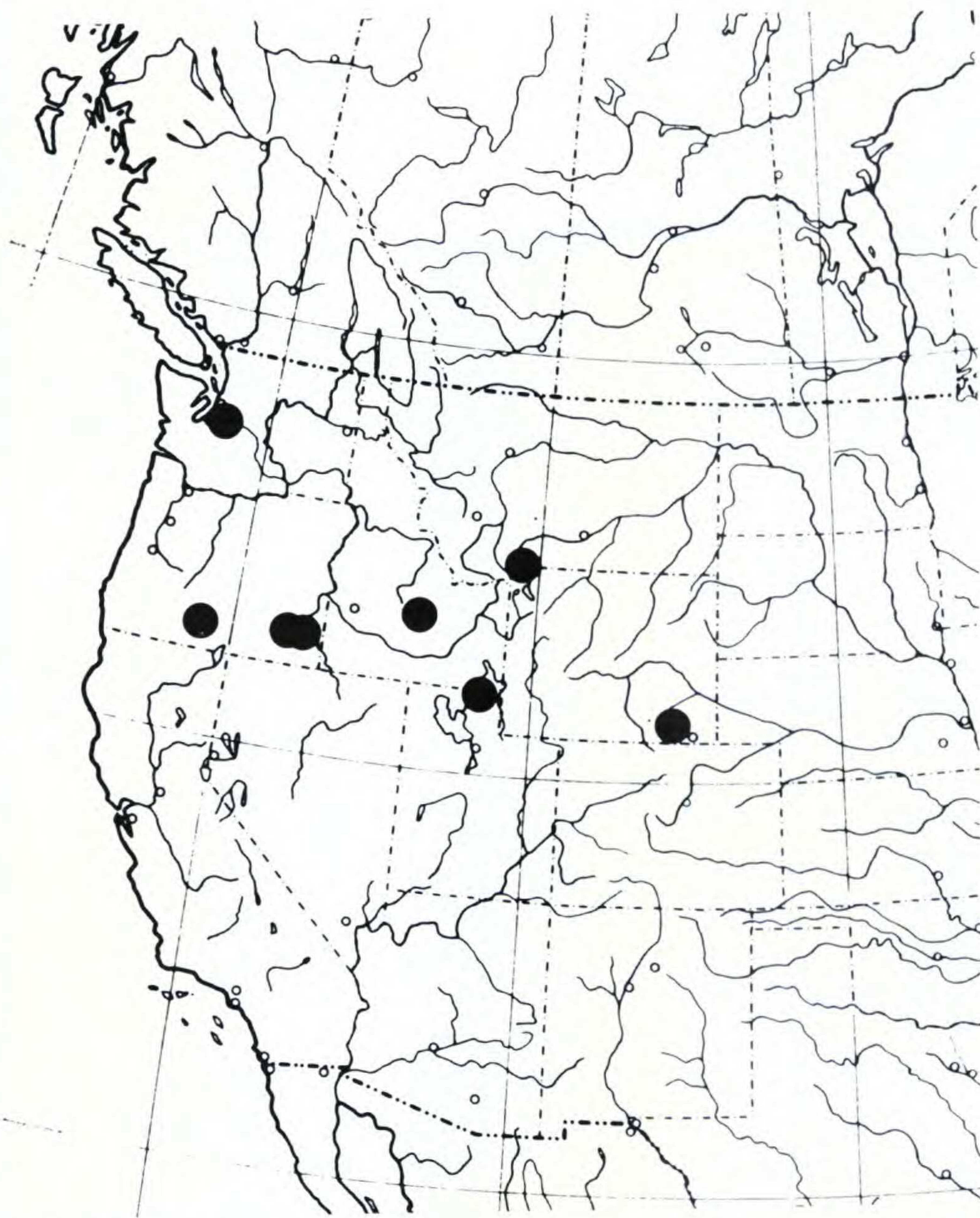


Fig. 9. Map of northwestern United States showing documented distribution of *Potamogeton foliosus* var. *fibrillosus*.

REPRESENTATIVE SPECIMENS

UNITED STATES: **Idaho:** BLAINE CO.: Russian John Ranger Station, *Macbride & Payson* 3790 (UC). **Oregon:** HARNEY CO.: warm spring, near Burns, *Henderson* 8867 (GH); irrigating ditch at Frenchglen, *Thompson* 12068 (NY). KLAMATH CO.: N end of Klamath Marsh, *Peck* 21954 (UC). MALEUR CO.: Otis Creek, *Leiberg* 2340 (GH, US). **Utah:** CACHE CO.: stream, 3 mi. NE of Logan, *Maguire* 16685 (CAN, MO, NY); stream, 2 mi. NW of Logan, *Maguire* 21578 (DAO, F, GH, MICH, MO, NY, US). **Washington:** PIERCE CO.: outlet, Lake Spanaway, near Tacoma, *Thompson* 9657 (GH, NY); unknown locality, Washington Territory, *Brandegge* 1127 (GH, UC). **Wyoming:** ALBANY CO.: N. fork of Pole Creek, *Porter* 3474 (NY, US). PARK CO.: Firehole River, *Jepson* 2540 (GH); Firehole Canyon, Firehole River, *Haynes* 3848 (ILL, OS, PH, UC, US); Midway Geyser Basin, Firehole River, *Haynes* 3850 (GH, MICH, MO, NY, OS); Upper Geyser Basin, *Richardson* (GH); Upper Nez Perce Creek, *Haynes* 3849 (MICH, OS).

6. **Potamogeton clystocarpus** Fern., Mem. Amer. Acad. Arts 17: 79. 1932. TYPE: *J. A. Moore & J. A. Steyermark* 3088, pool in rock, Little Aguja Canyon, Davis Mts., 1575 ft. Jeff Davis Co. Texas, (holotype, GH!; isotypes, MICH!, MO!, NY!, PH!, US!).

Stem light green to brown, terete to slightly compressed, rarely ridged, to 57 cm long, 0.5-0.7 mm diam. Leaves green, 3 (-5)-nerved, 3.2-7.8 cm long, 0.7-1.7 mm wide; apex acute; glands usually present, white to gold, 0.2-0.3 mm diam; lacunae to 4 rows each side of midrib, rarely absent; lateral nerves joining midrib 0.2-0.4 mm below apex. Stipules brown, delicate, not shredding at tip, usually convolute, to 6.2 mm long, 0.5-0.8 mm diam. Winter buds unknown. Peduncles cylindrical, axillary to terminal, erect, 3.2-4.8 cm long, 0.3-0.5 mm diam. Spike capitate to cylindric, 5.5-7.5 mm long, 3.0-5.7 mm diam; verticels 3, 1.5-1.7 mm apart. Perianth segments 1.7-2.0 mm long, 1.5-1.8 mm wide. Fruit brown to yellow-green, dorsally and laterally keeled, 2.0-2.2 mm long, 1.7-1.8 mm wide; keels ridged, without undulations, to 0.2 mm high; beak central, 0.5-0.6 mm long, 0.2-0.4 mm diam; sides depressed, with 1-3 tubercles near base; wall texture rough. Chromosome number unknown.

Distribution: Known only from the type locality. Fruiting from early May to mid-June. Fig. 10.

Illustrations: Fernald (1932, plate 15.30, fig. 5) ; Ogden (1966, plate 51).

Potamogeton clystocarpus was named by Fernald (1932), based on the "gibbous-tuberculate-based fruits." He suggested the fruits were "so similar to those of the western Eurasian and African *P. trichoides* C. & S. in having basal bosses that they might easily pass as fruits of that species. *P. trichoides*, however, as its name implied, has very bristle-tipped leaves . . . *P. clystocarpus* cannot be referred to it." No other North American pondweed, to my knowledge, has fruits with the basal "bosses." In this character, *P. clystocarpus* is quite distinct. But, as with other *Pusilli*, it is almost impossible to identify with sterile material!

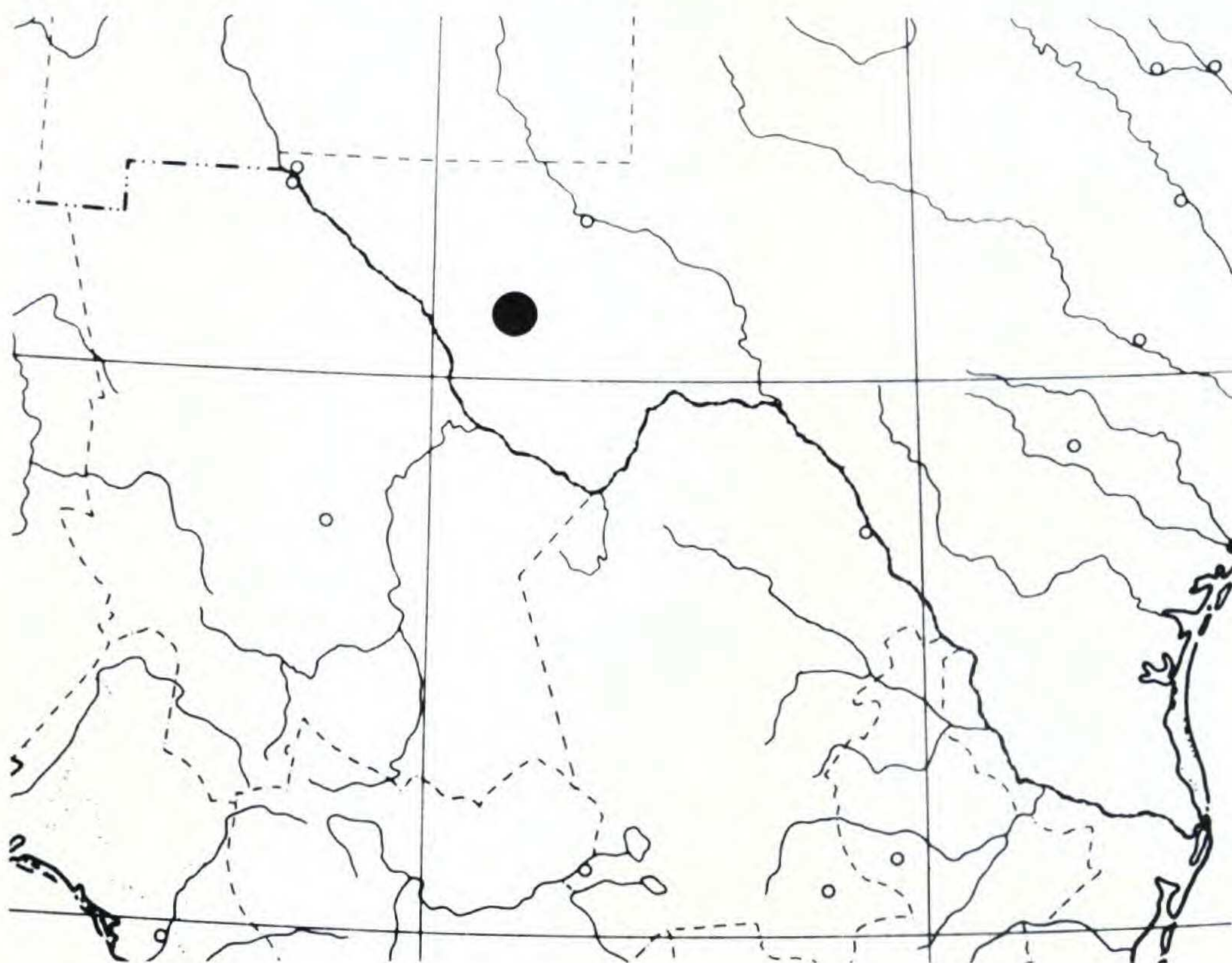


Fig. 10. Map of southwestern North America showing documented distribution of *Potamogeton clystocarpus*.

REPRESENTATIVE SPECIMENS

UNITED STATES: Texas: JEFF DAVIS CO.: Little Aguja Canyon, Davis Mts., *Palmer* 34526 (MO, NY, PH), *Correll & Ogden* 25070 (NYS, UC).

7. *Potamogeton pusillus* L., *Species Plantarum* 1: 127. 1753.

Stems pale green to olive, terete to slightly compressed, smooth to slightly ridged, 18-150 cm long, 0.1-0.7 mm diam. Leaves pale green to olive, rarely rufescent, delicate to coarse, 1-3 (-5)-nerved, 0.9-6.5 cm long, 0.2-2.5 mm wide; apex subulate to obtuse; glands present or absent, green, gold, brown, or rarely white, to 0.5 mm diam; lacunae absent or to 5 rows each side of midrib; lateral nerves, when present, joining midrib 0.1-1.0 (-2.0) mm below apex. Stipules brown to green or white, delicate, rarely appearing fibrous, not shredding at tip, connate or convolute, 3.1-9.2 mm long, 0.2-0.7 mm diam. Winter buds common, lateral or terminal, 0.9-3.2 cm long, 0.3-1.8 mm wide; inner leaves rolled into a hardened fusiform structure; outer leaves 1-3 per side, subulate to obtuse, without corrugations at base. Peduncles filiform to slightly clavate, axillary or terminal, mostly erect, rarely recurved, 0.5-6.2 (-6.6) cm long, 0.2-0.7 mm diam. Spikes capitate to cylindric, 1.5-10.1 mm long, 0.7-5.2 mm diam; verticels 1-3 (-4), 1.2-4.7 mm apart. Perianth segments 0.7-1.7 mm long, 0.5-1.2 mm wide. Fruit green to brown, without keels, 1.5-2.2 mm long, 1.2-1.6 mm wide; beak forward or central, 0.1-0.6 mm high, 0.2-0.5 mm diam; sides rounded; wall texture smooth or rough.

Potamogeton pusillus has been interpreted variously by botanists. Bennett (1890-1894; 1900-1904) and Morong (1893), for example, considered the taxon to consist of two species, one being divided into several varieties. Hagstrom (1916), on the other hand, divided the taxon into several poorly defined species, with two of these — *P. panormitanus* [var. *pusillus*] and *P. pusillus* [var. *tenuissimus*] — being split into many infraspecific taxa. These two species were separated by the connate versus convolute character of the stipule. Fernald (1932) took the intermediate position and

recognized three species — *P. panormitanus* [var. *pusillus*], *P. gemmiparus* [var. *gemmiparus*], and *P. pusillus* [var. *tenuissimus*]. He divided *P. panormitanus* into two varieties and *P. pusillus* into six varieties. These varieties were based on the size of the leaf, apex shape, and number of lacunae bordering the midrib. The latter concept of the taxon was accepted until Dandy and Taylor (1938), after studying the type specimen of *P. pusillus* in the Linnaean herbarium, decided that the name *P. pusillus* actually should be applied to the taxon which had been passing as *P. panormitanus*. For the taxon which had been passing as *P. pusillus*, the next available name in the specific rank was *P. berchtoldii* Fieber. Fernald (1940) finally made the combinations of various varieties to conform with the revised nomenclature. This is the concept that appeared in the eighth edition of Gray's Manual (Fernald, 1950). Gleason and Cronquist (1963), however, did not accept *P. pusillus* and *P. berchtoldii* as two distinct species. They, instead, suggested that although this character may be good for distinguishing certain species, there was no reason to assume that both states of the stipule and gradations between could not occur within one species. As I indicated earlier, a single plant may produce two sets of leaves during one growing season. The first set may have obtuse leaves with 4-5 rows of lacunae; the second, instead, would probably have acute leaves with 1-3 rows of lacunae. In the early summer, this plant would resemble var. *mucronatus* [of Fernald, 1932] and in the late summer, it would resemble var. *tenuissimus* [of Fernald, 1932]. For this reason and because of the ecological variability as explained by Sculthorpe (1967), I have decided to recognize only three taxa.

Fernald (1950) suggested that useful characters in distinguishing *Potamogeton pusillus* from *P. berchtoldii* were length of inflorescence, branching of the plant, and whether the fruit is wider at, above, or below the middle. Voss (1972) had noticed that fruiting specimens with connate stipules [*P. pusillus* var. *pusillus*] from Michigan often

lacked glands. Ogden (personal communication) suggested that the presence or absence of lacunae along the midrib often is a reliable character for distinguishing the species. Eighty specimens were examined for the characters mentioned above and other features. Some correlation, although slight, was noticed between the stipule character, the diameter of the glands, and the number of lacunae bordering the midrib. However, for the majority of the characters measured, little or no correlation was observed. Regardless of the inconsistency of the stipule character, the shape of the inflorescence and of the fruit, and the length of peduncle seem to be associated. This is not to say that intermediates do not occur, because they do! In their extremes, the two entities can be separated by the length of the inflorescence, the shape of the fruit, the length of the peduncle, the number of lacunae bordering the midrib, the presence and size of nodal glands, and, finally, the connation of the stipules. No one character can definitely be depended upon, but by using a combination of as many of the above mentioned characters as are present on the plant, one can place the specimen into the correct taxon 70-80% of the time. The remaining 20-30%, however, are almost impossible to identify without depending upon one character taxonomy. Also, var. *tenuissimus* has a more northerly distribution, e.g. into Alaska, and var. *pusillus* has a more southerly distribution, e.g. into Mexico. Because of the morphological integradation and the slight range differences, I have decided to place the two taxa at the varietal level.

When in fruit, *Potamogeton pusillus* should not be confused with any other pusilloid. Its fruit, lacking a keel, a wing, or basal warts, and its delicate stipules separate it from all other species. However, in the sterile state, identification is not so easy. Vegetatively, it closely resembles *P. foliosus*, *P. clystocarpus*, and some individuals of *P. hillii*. I can give no morphological characters which serve to separate *P. pusillus* from *P. clystocarpus* if fruits are lacking. If the specimen is from areas other than western Texas, one can assume the specimen is not *P. clystocarpus*, although

this may not be a valid assumption. The stipules of *P. pusillus*, usually lacking slightly fibrous veins, often serve to distinguish the species from *P. hillii* and *P. foliosus*. However, the stipules of the two latter species may, on occasions, appear to lack the fibrous veins. In this instance, the species are impossible to separate. Therefore, one should always make an effort to collect fertile material!

7a. *Potamogeton pusillus* var. *pusillus*

Potamogeton pusillus L., Species Plantarum, 128. 1753. *P. pusillus* var. *typicus* Fern., Mem. Amer. Acad. Arts 17: 81. 1932. TYPE: Europe. (holotype, LINN; photograph of holotype, OS!).

Potamogeton panormitanus Ant. Biv. Bern. in And. Biv. Bern. Nuove piante inedite del barone Ant. Bivona Bernardi 6. 1838. (publication not seen). *P. pusillus* var. *panormitanus* (Ant. Biv. Bern. in And. Biv. Bern.) Morong, Mem. Torrey Bot. Club 3: 46. 1893. TYPE: (location unknown).

Potamogeton panormitanus var. *major* Ant. Biv. Bern. in And. Biv. Bern., Nuove piante inedite del barone Ant. Bivona Bernardi 6. 1838. (publication not seen). TYPE: (location unknown).

Potamogeton panormitanus var. *minor* Ant. Biv. Bern. in And. Biv. Bern. Nuove piante inedite del barone Ant. Bivona Bernardi 6. 1838. (publication not seen). *P. pusillus* var. *minor* (Ant. Biv. Bern. in And. Biv. Bern.) Fern. & Schubert, Rhodora 50: 154. 1948. TYPE: (location unknown).

Potamogeton pusillus var. *vulgaris* Fries, Novitiae Florae Suecicae 2nd ed. 49. 1828. TYPE: (type not located), application of the name is from the illustration of *Potamogeton pusillus* L. In Smith, English Bot. 2: pl. 215. 1794!

Potamogeton pusillus var. *vulgaris* subvar. *interruptus* Robbins in Watson, Bot. U. S. Geol. Expl. Fortieth Parallel 338. 1871. TYPE: S. Watson, 1137, Parley's Park in the Wasatch, 6,000 ft. [Wasatch Co.], Utah, (holotype, NY!; isotype, US!).

Stems green to brownish, mostly terete, slightly ridged, 18-150 cm long, 0.2-0.7 mm diam. Leaves pale green, rarely olive, delicate, 1-3-nerved, 1.4-6.5 cm long, 0.5-1.9 mm wide;

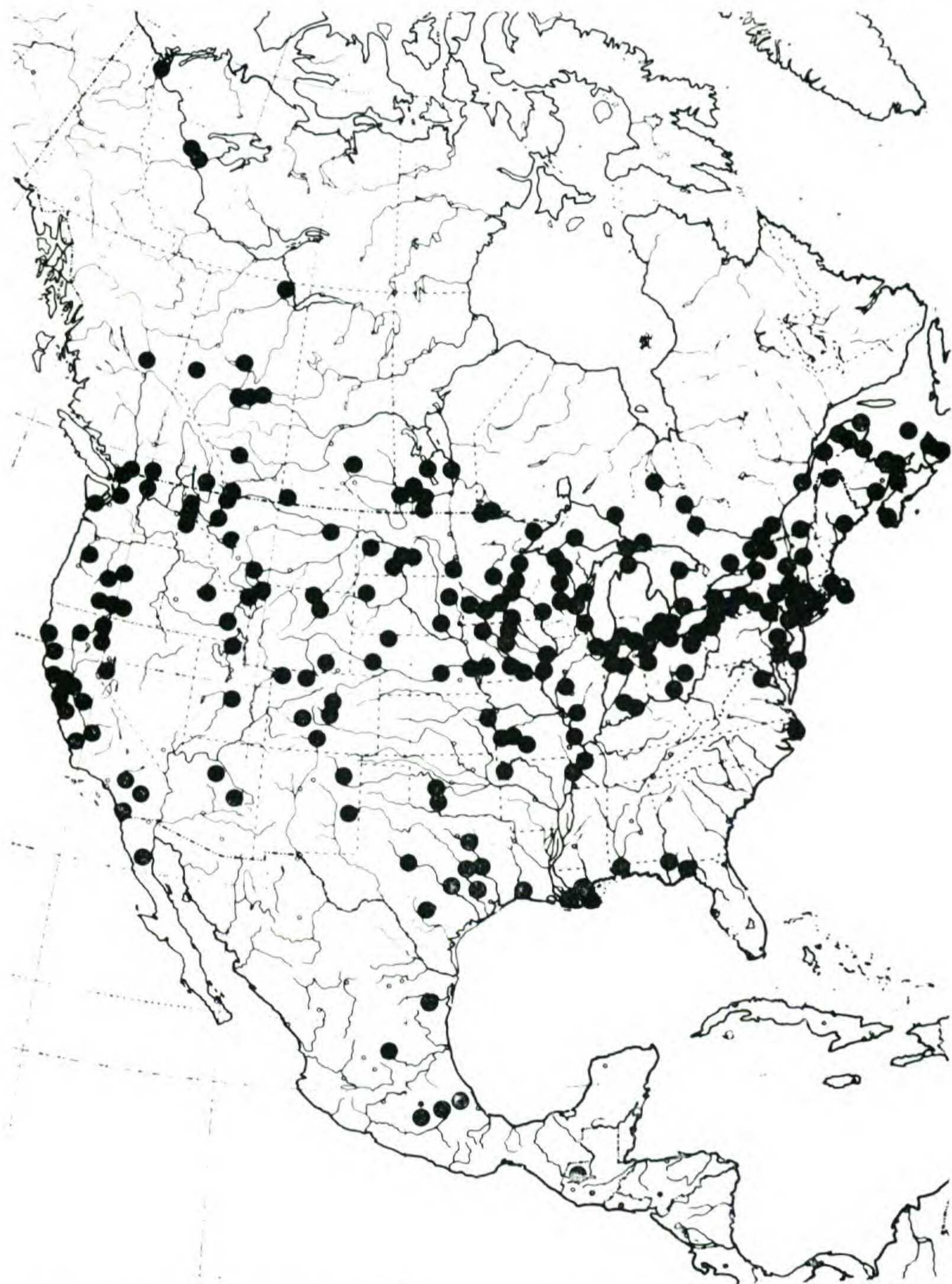


Fig. 11. Map of North America showing documented distribution of *Potamogeton pusillus* var. *pusillus*.

apex acute or rarely apiculate, rarely with a bristle; glands often present, green, gold, brown, or rarely white, to 0.3 mm diam; lacunae absent or to 2 rows each side of midrib; lateral nerves joining midrib 0.1-0.7 mm below the apex. Stipules greenish to brown, delicate, rarely fibrous, usually connate, 2.2-9.2 mm long, 0.2-0.7 mm diam. Winter buds uncommon, lateral or terminal, 0.9-1.5 cm long, 0.3-1.8 mm wide; outer leaves 1-2 per side, acute to apiculate. Peduncles cylindric, axillary, to lower or upper leaves, rarely recurved, 1.0-6.2 cm long, 0.2-0.7 mm diam. Spikes cylindric, 2.5-10.1 mm long, 1.2-4.7 mm diam; verticels 2 or 3 (-4), usually interrupted, 1.4-4.5 mm apart. Perianth segments 1.0-1.5 mm long, 0.7-1.2 mm wide. Fruit green to brown, usually wider above the middle, 1.5-2.2 mm long, 1.2-1.5 mm wide; keel absent; beak forward, rarely central, 0.1-0.6 mm high, 0.2-0.5 mm diam; sides rounded, usually centrally depressed; wall texture smooth. Chromosome number $2n = 26$ (Palmgren, 1939).

Distribution: From central British Columbia to Nova Scotia, south to northern Guatemala and western Florida. Fruiting from early May to late September. Fig. 11.

Illustrations: Fernald (1932, pl. 9; 10; 29, fig. 7, 8; 33, fig. 4, 5; 39, fig. 10).

REPRESENTATIVE SPECIMENS

CANADA: **Alberta:** Wood Buffalo Park, *Raup* 1568 (CAN, GH, NY, UC, US). **British Columbia:** pond near Similkameen River, *Macoun* 70317 (F, GH, NY). **Manitoba:** Desford, pothole, *Love & Love* 6092 (DAO, ILL, US). **New Brunswick:** KINGS CO.: Westfield, Ingleside, cove in St. John River, *Fernald* 1618 (GH, NY). **Northwest Territories:** MACKENZIE DIST.: Norman Wells, MacKenzie River, *Cody & Guttridge* 7631 (F, NY, US). **Nova Scotia:** CAPE BRETON CO.: Fort Louisbourg, *Smith et al.* 8281 (CAN, DAO). **Ontario:** OTTAWA CO.: Ottawa, Rideau Canal, *Fletcher* (MO, NY, PH). **Prince Edward Island:** Tignish, pools and ponds, *Fernald et al.* 6776 (CAN, K, NY). **Quebec:** Magdalen Islands, Grindstone Island, *Fernald et al.* 6780 (GH, K, NY, US), *Fernald et al.* 6781 (GH, NY, PH, US). **Saskatchewan:** MAPLE CREEK DIST.: 14.7 mi. N of Govenlock, middle Creek, *Bird* 1022 (DAO). **GUATEMALA:** **Quiche Dept.:** Quiche, pond, *Muenschner* 12085 (UC). **MEXICO:** **Baja California:** La Encantada, Sierra San Pedro Martir, *Wiggins & Demaree* 4906 (GH, MU, US). **Hidalgo:**

DIST. MOLANGO: Molango, Lake Atexca, *Moore* 3470 (UC). **Morelos:** Zempoala National Park, Lake Zempoala, *Moore* 3435 (GH, US). **Puebla:** vicinity of Puebla, Laguna de San Baltasar, *Arsene* 1323 (US). **San Louis Potosi:** San Louis Potosi, *Schaffner* 533 (K, NY). **Tamaulipas:** vicinity of San Jose, Sierra de San Carlos, *Bartlett* 10397 (F, MICH, US). **Veracruz:** Los Molinos, Perote, pond, *Balls & Gourlay* (K, MICH, UC, US). **UNITED STATES:** **Alabama:** 7-8 mi. NE of Mobile, Chuckfey Bay, *Hotchkiss & Ekvall* 3902 (US). **Arizona:** GILA CO.: Young's Ranch, *Lemmon* (K, MO, NY, UC, US). **Arkansas:** MISSISSIPPI CO.: S. of Hornersville, Missouri, *Metcalf* 644 (GH, NY, US). **California:** HUMBOLDT CO.: Eel River, near Fernbridge, *Harris* 808 (CAN, DAO, F, GH, ILL, MICH, MO, NY, PH, UPS, US). **Colorado:** ROUTT CO.: ponds between Hayden and Craig, *Porter* 6563 (CAN, DAO, NY, UC, UPS). TELLER CO.: base of Pike's Peak, Lake Osborne, *Parry* (GH, MO, NY). **Connecticut:** MIDDLESEX CO.: Grove Beach, creek, *Enquist* 366 (NY). **Florida:** JACKSON CO.: N of Sneads, Lake Seminole, *Adams* 445 (US). **Idaho:** CUSTER CO.: 15 mi. N of Challis, ditch, *Hitchcock et al.* 23839 (DAO, ILL, NY, UC). **Illinois:** COOK CO.: South Chicago, ditches, *Hill* 89-1875 (F, ILL). **Indiana:** CASS CO.: Lake Cicott, *Deam* 49306 (GH). **Iowa:** CLAY CO.: Lake Twp, Round Lake, *Hayden* 10120 (GH, MO, NY, PH, UC, US). **Kansas:** DOUGLAS CO.: 1½ mi. E and ½ mi. N of Lawrence, ponds, *Richards* 3079 (NY). **Louisiana:** CAMERON PAR.: Sabine National Wildlife Refuge, *Valentine* (OS). **Maine:** AROOSTOOK CO.: Oxbow, Aroostook River, *Oaden* 2661 (OS). **Maryland:** CECIL CO.: Blairs Shore, Elk River, *Long* 57093 (PH). **Massachusetts:** BERKSHIRE CO.: New Marlboro, Lake Buel, *Churchill* (GH, MO). **Michigan:** EMMET CO.: small arm of Carp Lake, *Haynes* 3370 (CAN, FSU, GH, ILL, MICH, MO, MSU, NY, OS, PH, UC, US, WVA). *Haynes* 3706 (ILL, OS). **Minnesota:** ST. LOUIS CO.: Armstrong, near Ely, *Jones* 18543 (ILL, NY, US). **Missouri:** LACLEDE CO.: Gasconade River, between Falcon and Nelio, *Steyermark* 13913 (GH, MO). **Montana:** GALLATIN CO.: ca. 12 mi. NW of West Yellowstone, Hegben Lake, *Haynes* 3841 (OS). LAKE CO.: 0.2 mi. SE of Nine-Pipes Reservoir, pot-hole, *Hitchcock et al.* 23980 (CAN, F, ILL, NY, UC). **Nebraska:** CHERRY CO.: 30 mi. S of Valentine, small pond, *Porter* 6445 (DAO, NY, UPS). **Nevada:** STOREY CO.: vicinity of Reno, Sparks, irrigation ditch, *Hitchcock* 443 (GH, US). **New Jersey:** SUSSEX CO.: Catfish Pond, *Griscom* 9750 (GH). **New Mexico:** SAN MIGUEL CO.: Montezuma, Peterson Reservoir, *Drouet & Richards* 3308 (F, GH). **New York:** ST. LAWRENCE CO.: Lisbon, Sucker Brook, *Phelps* 269 (CAN, GH, NY, US). **North Carolina:** DARE CO.: Currituck Sound, inlet S of Duck, *Radford* 5758 (DAO, UC). **North Dakota:** BURLEIGH CO.: 7 mi. E of Bismark, slough, *Metcalf* 356 (US). **Ohio:** PORTAGE CO.: ca. 5½ mi. NW of Ravenna, small pond, *Haynes* 3450 (OS). **Oklahoma:** COMANCHE CO.: Wichita Mountains Wildlife

Refuge, Lake Quannah Parker, *McMurry* 1219 (NY). Oregon: WHEELER CO.: 15 mi. E of Mitchell, roadside pond, *Hitchcock et al.* 23779 (CAN, DAO, F, ILL, NY, UC). Pennsylvania: BERKS CO.: 1 mi. NW of Moselem Springs, *Brumbach* 2841 (PH). South Dakota: CODINGTON CO.: outlet of Lake Kampeska, *Over* 17149 (US). Tennessee: OBION CO.: Walnut Log, *Sharp* 7933 (OS). Texas: TRAVIS CO.: Colorado River, ca. 5 mi. below Austin, *Barkley* 13313 (F, GH, MO, PH, UC). WALLER CO.: Hempstead, *Hall* 620 (F, K, MO, NY, US). Utah: CACHE CO.: 1 mi. W of Logan, marsh, *Maguire* 13883 (CAN, GH, DAO). Vermont: WINDSOR CO.: Windsor, mill pond, *Hellquist* 1813 (Boston State College). Virginia: FAIRFAX CO.: Dyke, *Metcalf & Sperry* 1688 (GH). Washington: GRAYS HARBOR CO.: slough near ocean beach, *Otis* 2116 (GH, NY, PH, UC). Wisconsin: LA CROSSE CO.: Lake Onalaska, *Hartley* 1826 (DAO, F, ILL, US). Wyoming: ALBANY CO.: Laramie River E of Lookout, *Porter* 6352 (DAO, MO, NY, UPS).

7b. *Potamogeton pusillus* var. *tenuissimus* Mert. & Koch in Röhling, 857. 1823. TYPE: (location unknown).

Potamogeton tenuissimus (Mert. & Koch in Röhling) Reichen. Icones Florae Germanicae Helveticae 7: 14. 1845. *P. berchtoldii* var. *tenuissimus* (Mert. & Koch in Röhling) Fern. & Schubert, Rhodora 42: 246. 1940.

Potamogeton berchtoldii Fieber, in Berchtold, Oekon.-tech. Flora Bohmens, 277. 1838. TYPE: (location unknown).

Potamogeton berchtoldii var. *mucronatus* Fieber in Berchtold, Oekon.-tech. Flora Bohmens 277. 1838. *P. pusillus* var. *mucronatus* (Fieber) Graebner in Ascherson & Graebner, Das Pflanzen. 4(11): 115. 1907. TYPE: (location unknown).

Potamogeton berchtoldii var. *acuminatus* Fieber in Berchtold, Oekon.-tech. Flora Bohmens 278. 1838. TYPE: (location unknown).

Potamogeton pusillus var. *polyphyllus* Morong, Bot. Gaz. (Crawfordsville) 5: 51. 1880. *P. berchtoldii* var. *polyphyllus* (Morong) Fern. Rhodora 42: 246. 1940. TYPE: *T. Morong*, oozy pool in South Natick, [Middlesex Co.], Massachusetts, (holotype, NY!).

Potamogeton pusillus var. *elongatus* Ar. Benn., in Macoun, Cat. Canadian Plants 4: 371. 1888. TYPE: *J. Macoun* 4140, Spullamasheen River at and above Enderby, British Columbia, Canada, (holotype, K[?]; isotype, GH!). *P. pusillus*

var. *capitatus* Ar. Benn., *nom. illeg.*, J. Bot. 39: 201. 1901. (Superfluous when published).

Potamogeton pusillus var. *cuspidatus* G. Fisher, Ber. Bayer. Bot. Ges. 11: 116. 1907. TYPE: (location unknown).

Potamogeton lacunatus Hagstrom, Kongl. Svenska Vetenskapsakad. Handl. 55(5): 120. 1916. *P. pusillus* var. *lacunatus* (Hagstrom) Fern. Mem. Amer. Acad. Arts 17: 85. 1932. *P. berchtoldii* var. *lacunatus* (Hagstrom) Fern. Rhodora 42: 246. 1940. TYPE: *T. Morong*, Ashland, in lacu Wauhakune, [Middlesex Co.], Massachusetts, (lectotype here designated, UPS!).

Potamogeton turionifera f. *tenuis* Hagstrom, Kongl. Svenska Vetenskapsakad. Handl. 55(5): 91. 1916. TYPE: *J. Macoun*, Algonquin Park, Cache Lake, Ontario, Canada, (lectotype here designated, C!; isolectotypes, C!, CAN!, GH!).

Potamogeton turionifera f. *mucronulatus* Hagstrom, Kongl. Svenska Vetenskapsakad. Handl. 55(5): 91. 1916. TYPE: *J. Macoun*, Ottawa, Brigham's Creek, Ontario, Canada, (holotype, C!; isotypes, C!, CAN!, GH!).

Potamogeton pusillus var. *colpophilus* Fern. Mem. Amer. Acad. Arts 17: 90. 1932. *P. berchtoldii* var. *colpophilus* (Fern.) Fern. Rhodora 42: 246. 1940. TYPE: *J. F. Collins*, *M. L. Fernald*, & *A. S. Pease*, brackish pools and dead waters near the mouth of Dartmouth River, Gaspé Co., Quebec, Canada, (holotype, GH!; isotypes, CAN!, NY!, US!).

Stem light green to olive, terete to slightly compressed, usually smooth, 22-74 cm long, 0.1-0.5 mm diam. Leaves pale green to olive, rarely rufescent, delicate, 1-3 (-5)-nerved, 0.9-5.4 cm long, 0.2-2.5 mm wide; apex acute to obtuse; glands usually present, green to brown or white, to 0.4 mm diam; lacunae usually present, 1-5 rows each side of midrib; lateral nerves, when present, joining midrib 0.3-1.0 (-2.0) mm below apex. Stipules brown to green, rarely white, delicate, mostly convolute, 3.1-5.0 mm long, 0.2-0.5 mm diam. Winter buds common, lateral or terminal, 1.2-3.2 cm long, 0.7-1.2 mm wide; outer leaves 1-3 per side, acute to obtuse. Peduncles cylindrical to slightly clavate,

axillary or terminal, rarely recurved, 0.5-4.6 (-6.6) cm long, 0.2-0.7 mm diam. Spikes capitate to cylindric, 1.5-7.2 mm long, 0.7-5.2 mm diam; verticels 1-3, when of 2 or 3, then these crowded, 1.2-2.5 mm apart. Perianth segments 0.7-1.0 mm long, 0.5-0.7 mm wide. Fruit green to brown, usually wider at or below the middle, 1.6-2.1 mm long, 1.2-1.5 mm wide; keels absent; beak usually central, rarely forward, 0.2-0.5 mm long, 0.2-0.4 mm diam; sides usually rounded, rarely centrally depressed; wall texture smooth. Chromosome number, $n = 13$; $2n = 26$ (Taylor & Mulligan, 1968).

Distribution: Central Alaska to Labrador, south to California and northern Florida. Fruiting from early June to late September. Fig. 12.

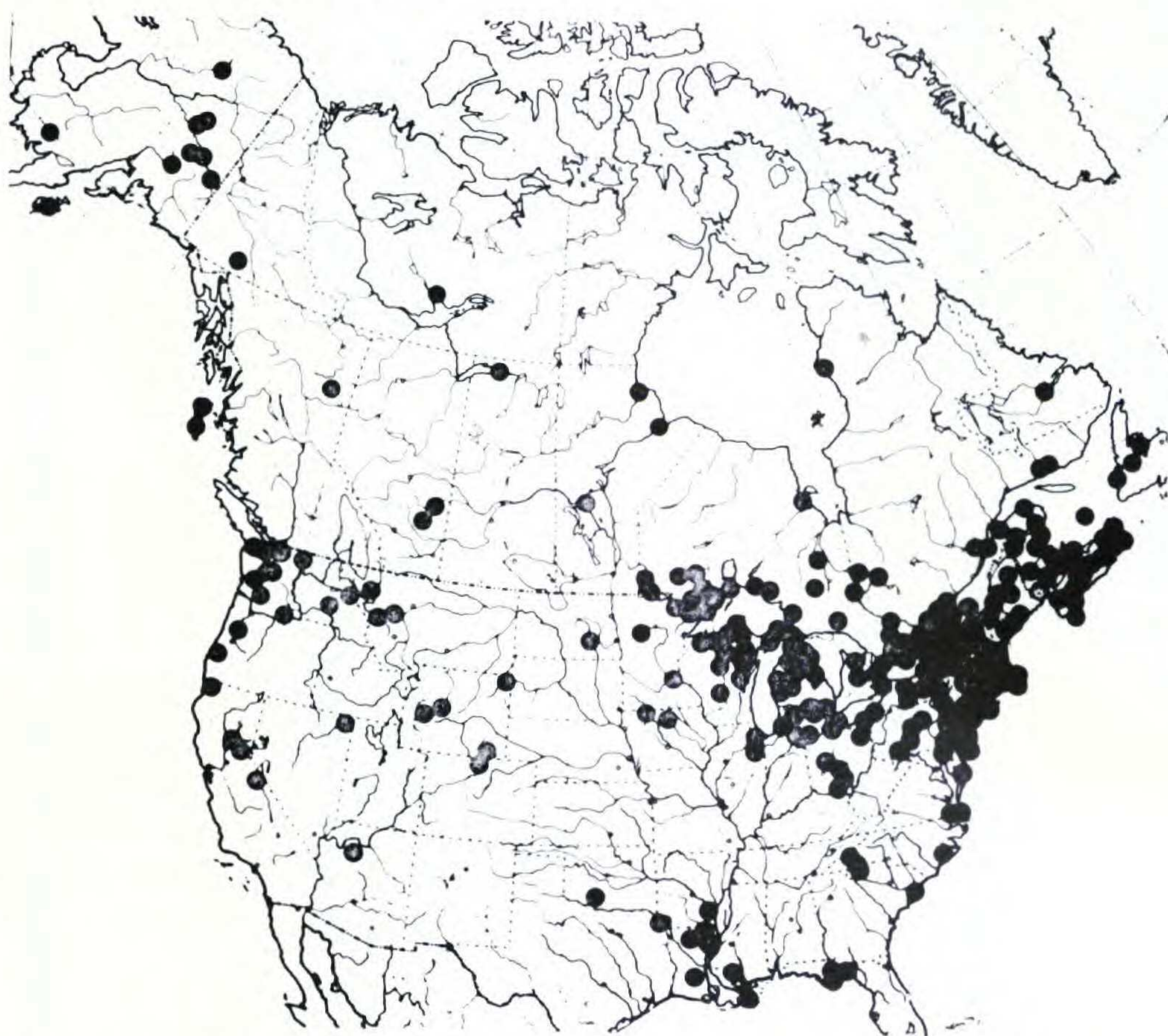


Fig. 12. Map of North America showing documented distribution of *Potamogeton pusillus* var. *tenuissimus*.

Illustrations: Fernald (1932, pl. 16-20; 30, fig. 6-9; 31, fig. 1; 35; 39, fig. 9).

REPRESENTATIVE SPECIMENS

CANADA: **Alberta:** CRAIGMYLE DIST.: Craigmyle, *Brinkman* 538 (US). **British Columbia:** QUEEN CHARLOTTE ISLANDS: Graham Island, 2 mi. NW of Tlell, $n = 13$, *Calder & Taylor* 35688 (DAO); Moresby Island, White Swan Lake, $2n = 26$, *Calder & Taylor* 35297 (DAO). **VANCOUVER ISLAND:** Lost Lake near Victoria, *Macoun* (CAN, GH, NY, US). **Labrador:** Goose Bay, $53^{\circ}20'N$, $60^{\circ}09'W$, *Gillett & Findlay* 5910 (DAO, NY). **Manitoba:** CHURCHILL DIST.: Gillman Lake, *Schofield* 1524 (DAO, GH). **New Brunswick:** CHARLOTTE CO.: Grand Manan, *Weatherby & Weatherby* 7284 (CAN, GH). **Newfoundland:** Harry's River, near Bay of St. George, *Fernald & Wiegand* 2453 (CAN, GH, NY). **Northwest Territories:** small pool 45.5 mi. WNW of Yellowknife, *Thieret & Reich* 7944 (CAN, F, OS, US). **Nova Scotia:** Sable Island, *St. John* 1125 (CAN, GH, NY, PH, US). **Ontario:** THUNDER BAY DIST.: Black Fox Lake, 12 mi. E of Terrace Bay, *Haynes* 3751a (OS); small lake 0.2 mi. NE of Coldwell, *Haynes* 3773 (ASC, CAN, FSU, GH, ILL, MICH, MO, MSU, NY, OS, PH, UC, US, WVA). **ESSEX CO.:** Fox's Pond, *Haynes* 3251 (OS), *Roberts* 1567 (OS). **Prince Edward Island:** QUEENS CO.: Watervale, *Erskine* (DAO). **Quebec:** MAGDALEN ISLANDS: ridges back of the Narrows, Alright Island, *Fernald et al.* 6778 (CAN, GH, K, NY, US). **Saskatchewan:** Cornwall Bay, Lake Atabaska, $59^{\circ}27'N$, $108^{\circ}27'W$, *Raup* 6633 (CAN, DAO, F, GH, NY). **Yukon:** Lewes River, Whitehorse, *Porsild & Breitung* 10644 (CAN).

UNITED STATES: **Alaska:** Goldstream Creek, 51 mi. N of Fairbanks, $65^{\circ}N$, $147^{\circ}30'W$, *Porsild & Porsild* 115 (CAN, GH, US). **Arkansas:** DREW CO.: Taxodium swamp, Tillar, *Demaree* 17394 (F, MO, NY, UC). **Arizona:** COCONINO CO.: Crater Lake, N of Mt. Agassy, *Lemmon* 3244 (GH). **California:** BUTTE CO.: cold spring, Jonesville, *Copeland* 604 (F, GH, K, MICH, MO, MU, NY, UC, US). **Colorado:** JACKSON CO.: Big Creek Lake, *Porter* 6433 (DAO, UPS). **Connecticut:** TOLLAND CO.: Stafford, *Morris* (F, GH, ILL, US). **Florida:** FRANKLIN CO.: 6 mi. NE of Carrabelle, *Adams* 442 (GH, UC, US). **Idaho:** SHOSHONE CO.: St. Maries River, 7 mi. SE of Clarkia, *Cronquist & Jones* 6038 (CAN, DAO, GH, ILL, MICH, NY, UPS, UC, US). **Illinois:** COOK CO.: South Chicago, *Hill* 88-1880 (ILL). **Indiana:** STEUBEN CO.: Crooked Lake, *Williams* (MO). **Iowa:** DICKINSON CO.: Manhattan Pond, Lakeville Twp. *Thorne* 13015 (UC). **Louisiana:** CALDWELL PAR.: Horseshoe Lake, 8 mi. NNW of Columbia, *Thomas* 4224 (OS). **Maine:** PENOBSBOT CO.: Stillwater River, Old Town, *Ogden & Steinmetz* 1600 (CAN, GH, NY, US). **Maryland:** HARFORD CO.: Spesutie Island, *Moldenke* 9398 (NY). **Massachusetts:** NORFOLK CO.: Charles River, Dedham, *Fernald & Svenson* 410 (CAN, DAO, F, GH, ILL, MICH, MO,

NY, UC, UPS, US). **Michigan:** CHEBOYGAN CO.: Black River, between its mouth and Alverno, *Haynes* 3378 (GH, ILL, OS, US), *Haynes* 3387 (OS); Marl Bay NW corner of Douglas Lake, *Haynes* 3712 (GH, ILL, MO, OS, UC), *Haynes* 3924 (OS). LUCE CO.: Bodie Lake, *Haynes* 3790 (OS); bog lake, 6½ mi. NE of Newberry, *Haynes* 3718 (OS). SCHOOLCRAFT CO.: Seney Wildlife Refuge, *Haynes* 3741 (OS). **Minnesota:** KOOCHICHING CO.: ditch 2 mi. E of Tilson Bay, Rainy Lake, *Moore & Moore* 11778 (DAO, GH, ILL, NY, UC, US). **Montana:** MISSOULA CO.: Ft. Missoula, *Hitchcock* 23968 (DAO, NY, UC). **Nevada:** ELKO CO.: Hot Creek Field, NE of Golliher Pasture, *Holmgren* 1401 (DAO, NY, UC). **New Hampshire:** CHESHIRE CO.: East Jaffrey, *Deane* (GH). **New Jersey:** CAMDEN CO.: Newton Creek, West Collingswood, *Adams* 370 (GH, MO, PH). **New York:** CORTLAND CO.: borrow pit just N of Little York, *Haynes* 3353 (OS). ESSEX CO.: outlet of Lake George, near Ticonderoga, *Haynes* 3336 (OS). SARATOGA CO.: Saratoga Lake, *Haynes* 3301 (OS), *Haynes* 3307 (OS). SUFFOLK CO.: Wading River, Riverhead, *Miller* (F, GH, US[4]). WARREN CO.: Dunham Bay, S end of Lake George, *Haynes* 3326 (GH, MICH, MO, NY, OS, US), *Haynes* 3329 (CAN, GH, ILL, MICH, MO, NY, OS, PH, UC, US); Lake Luzerne, *Haynes* 3812 (OS). **North Carolina:** CRAVEN CO.: 2 mi. SW of Blades, *Radford* 5856 (DAO, GH, NY). **North Dakota:** STUTSMAN CO.: Jim Lake, Pingree, *Mabbott* 316 (NY). **Ohio:** JACKSON CO.: Sec. 10, Jefferson Twp., *Roberts* 795 (CAN, LAF, MICH, OS, PH, US). LOGAN CO.: Indian Lake State Park, *Haynes* 3418 (OS). OTTAWA CO.: Middle Bass Island, Lake Erie, *Haynes* 3134 (OS); Squaw Harbor, Put-in-Bay, Lake Erie, *Haynes* 3127 (MICH). PORTAGE CO.: Twin Lakes, *Haynes* 3448 (OS). VINTON CO.: Lake Alma State Park, *Haynes* 3463a (OS). **Oklahoma:** COMANCHE CO.: Creek near Cache, *Stevens* 1369 (GH, ILL, K, MO, NY, US). **Oregon:** Porter Lake of Willamette River, 5 mi. S of Corvallis, *Wentz* 344 (MICH, MO, NY, OS, US). **Pennsylvania:** LUZERNE CO.: Lily Lake, *Small* (F, ILL, MU, NY). **Rhode Island:** NEWPORT CO.: Block Island, *Fernald et al.* 8448 (PH). **South Carolina:** GEORGETOWN CO.: Georgetown, *Forster* (NY). **Texas:** BOWIE CO.: Club Lake, 3 mi. W of New Boston, *Correll & Ogden* 25248 (LAF). **Vermont:** CALEDONIA CO.: beaver pond, Walden Twp., *Haynes* 3828 (MICH, OS). ESSEX CO.: Brunswick, *Eggleston* 1654 (GH, NY, US). LAMOILLE CO.: Wolcott Pond, Wolcott, *Haynes* 3826 (OS). **Virginia:** SUSSEX CO.: Chappell's Millpond, W of Lumberton, *Fernald & Long* 12236 (GH, PH). **Washington:** KLINKITAT CO.: Columbia River, Bingen, *Suksdorf* 2570 (F, GH, MO, US). **Wisconsin:** JUNEAU CO.: Glacial Lake Wisconsin, Cutler Twp. *Hartley* 8276 (GH, US). **Wyoming:** ALBANY CO.: Swastika Lake, Medicine Bow Mountains, *Porter* 6190 (DAO, GH, UC, UPS). CROOK CO.: pool 7 mi. N of Moorcroft, *Porter & Miller* 5974 (DAO, MO, UC, UPS).

Potamogeton perfoliatus × pusillus var. tenuissimus

Morong (1880) named *Potamogeton mysticus* based upon a collection from Mystic Pond, Massachusetts. The entity was said to have the habit of *P. perfoliatus*, a species of subsection *Perfoliati* of Hagstrom, but differed from this species by its delicate stature. Morong noted that the entity had never been known to fruit. Ogden (1943), however, based upon the extreme rarity of the entity and that it was not known to fruit, proposed it to be a hybrid with *P. perfoliatus* as one of its parents. He examined the stem anatomy of the entity, as well as studying the plants in the field. The stem anatomy appeared to be intermediate between *P. perfoliatus* and the *Pusilli*. At the one locality in which Ogden found the putative hybrid, *P. berchtoldii* var. *tenuissimus* [*P. pusillus* var. *tenuissimus*] was present. He thus suggested the entity to be a result of hybridization of *P. perfoliatus* and *P. berchtoldii* var. *tenuissimus* [*P. pusillus* var. *tenuissimus*]. Again, until the entity can be studied in depth, I am accepting the concept of Ogden.

SPECIMENS EXAMINED:

UNITED STATES: **Maine:** CUMBERLAND CO.: Scarboro, West Scarboro, Scarboro River, *Ogden et al.* 1731 (CAN, MO, NYS, US); Scarboro, West Scarboro, Stuart Brook, *Steinmetz & Martson* 539 (CAN, F, ILL, UC, US). **Massachusetts:** MIDDLESEX CO.: Medford, Mystic Pond, *Booth* (US), *Faxon* (ILL, US), *Morong* 11 Aug. 1879 (lectotype here designated, NY!; isoelectotypes, K!, MICH!, NY[3]!), *Morong* (K, NY). **North Carolina:** DARE CO.: Currituck Sound, inlet S of Duck, *Radford* 5757 (GH, NY, UC).

7c. Potamogeton pusillus var. gemmiparus Robbins in A. Gray Man. Bot. North. U. S. 5th ed. 489. 1867. **TYPE:** *Robbins*, Valley of the Blackstone, Uxbridge, Massachusetts, (lectotype here designated, NY!; isoelectotypes, GH!, NY!, PH!, US!).

Potamogeton gemmiparus (Robbins in A. Gray) Morong, Bot. Gaz. (Crawfordsville) 5: 51. 1880.

Stems pale green, terete, smooth, 30-140 cm long, 0.1-0.3 mm diam. Leaves pale green, uninervate, 1.1-6.0 cm long, 0.2-0.7 mm wide; apex subulate; glands gold, to 0.3 mm

diam; lacunae absent or to 2 rows each side of the midrib. Stipules white, convolute, 4.1-7.2 mm long, 0.2-0.4 mm diam. Winter buds abundant, terminal or lateral, 1.2-2.8 cm long, 0.7-1.5 mm wide; outer leaves 1-2 per side, subulate, much longer than inner. Peduncles cylindric, axillary or terminal, 1.1-2.8 cm long, 0.2-0.5 mm diam. Spike cylindric, 2.5-5.5 mm long, 1.2-3.0 mm diam; verticels 2-3, to 3.5 mm apart. Perianth segments 1.0-1.7 mm long, 0.7-0.8 mm wide. Fruit rare, greenish-brown, 1.9-2.0 mm long, 1.5-1.6 mm wide; beak central, 0.1-0.2 mm long, 0.2-0.3 mm diam; sides centrally depressed; wall texture rough. Chromosome number unknown.

Distribution: South-central Quebec south to central Massachusetts and Rhode Island. Fruiting late August to late September. Fig. 15.

Illustrations: Fernald (1932, pl. 12; 30, fig. 1; 34, fig. 1).

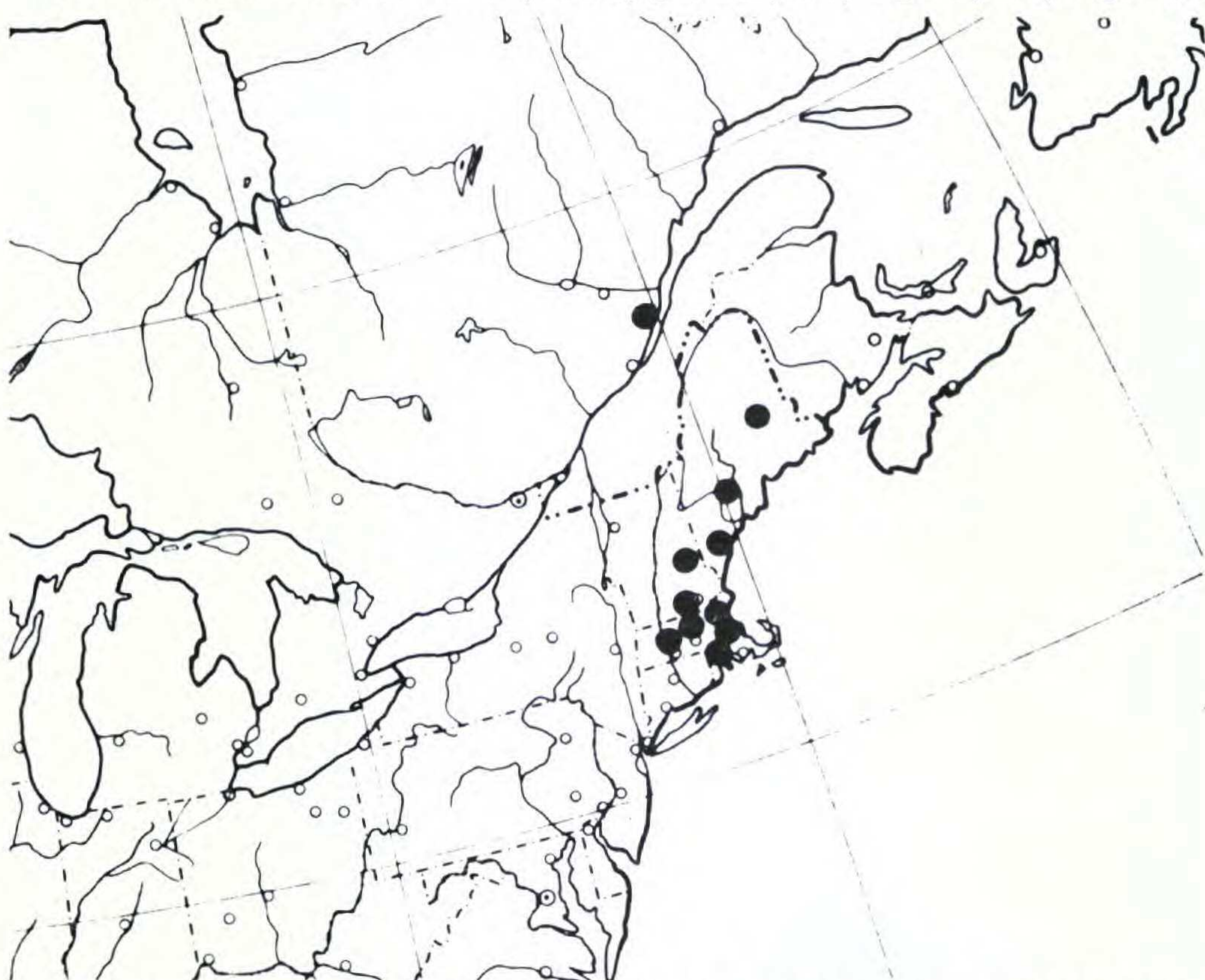


Fig. 13. Map of northeastern United States and southeastern Canada showing documented distribution of *Potamogeton pusillus* var. *gemmiparus*.

REPRESENTATIVE SPECIMENS

CANADA: Quebec: Saint-Tite, comte de Champlain, Lake Pierre-Paul *Gauthier* 2273 (GH, photo at DOA). UNITED STATES: Maine: CUMBERLAND CO.: Horseshoe Pond, North Fryeburg, *Hellquist* 4457 (MICH). KENNEBEC CO.: Belgrade Stream, Belgrade, *Hellquist* 4501 (MICH). PENOBSCOT CO.: Upper Stillwater, *Fernald* (UC, US), *Fernald* (GH). Massachusetts: HAMPSHIRE CO.: Amherst, *Jesup* (GH, NY). MIDDLESEX CO.: Charles River, South Natick, *Morong* (NY). NORFOLK CO.: Charles River, Dedham, *Fernald & Svenson* (GH). WORCESTER CO.: Uxbridge, *Morong* (CGE, F, ILL, MICH, MO, NY, US). New Hampshire: CARROLL CO.: Conway Lake, Eaton, *Hellquist* 4469 (MICH). HILLSBOROUGH CO.: Pine Island Pond, Manchester, *Krochmal* 265 (GH). Rhode Island: PROVIDENCE CO.: Central Pond, Ten Mile River, East Providence, *Collins* (GH).

8. *Potamogeton groenlandicus* Hagstrom, Kongl. Svenska Vetenskapsakad. Handl. 55(5): 127. 1916. TYPE: *Hartz*, Kingua Orpiksnit, 68°30', Greenland, (lectotype here designated, C!).

Potamogeton pusillus ssp. *groenlandicus* (Hagstr.) Boch. 1952. Meddel. Grønland 147(9): 44.

Stems light green, terete, smooth, 20-50 cm long, 0.2-0.3 mm diam. Leaves pale to deep green, 7-9 nerved, 2.6-8.8 mm long, 0.7-1.7 mm wide; apex acute to apiculate; glands usually present, white, 0.1-0.7 mm diam; lacunae absent or to three rows present each side of the midrib; lateral nerves joining the midrib 0.7-1.2 mm below the apex. Stipules brown, delicate, convolute, 4.5-19.1 mm long, 0.2-0.4 mm diam. Winter buds common, terminal or axillary, 4.2-8.4 cm long, 1.4-2.5 mm wide; inner leaves unmodified; outer leaves 2 per side, acute to apiculate, without corrugations at base. Peduncles rare, cylindric, terminal, ca 18.2 mm long, ca 0.5 mm diam. Spikes cylindric, ca 5.0 mm long, ca 3.5 mm diam; verticels 3, crowded, ca 1.0 mm apart. Perianth segments ca 1.1 mm long, ca 0.7 mm wide. Fruit unknown. Chromosome number unknown.

Distribution: Western Greenland. Flowering in late August. Fig. 14.

Illustrations: (apparently none).

In 1916, Hagstrom named *Potamogeton groenlandicus* from several sterile specimens. He distinguished this species from other *Pusilli* by its possessing 5-9 nerves per leaf. "In this respect," he stated, "this species constitutes an interesting link between the *Pusilli* and the *Oxyphylli* and would be ranked with the latter as well as with the former." He added that the ligules and leaf-apices, however, unite it with the *Pusilli*. Fernald (1932), after examining as many specimens as available [but not the Type], concluded the taxon to be conspecific with *P. pusillus* var. *mucronatus* [var. *tenuissimus*]. He stated that he had been unable to convince himself that the leaves were more than three-nerved. He added that this character alone does not warrant specific rank. I have examined the material at Copenhagen and at all the large herbaria of the United States and Canada. In my opinion, the leaves are 5-9 nerved. I agree with Fernald, however, that one vegetative character is not enough to separate two species, especially when one is

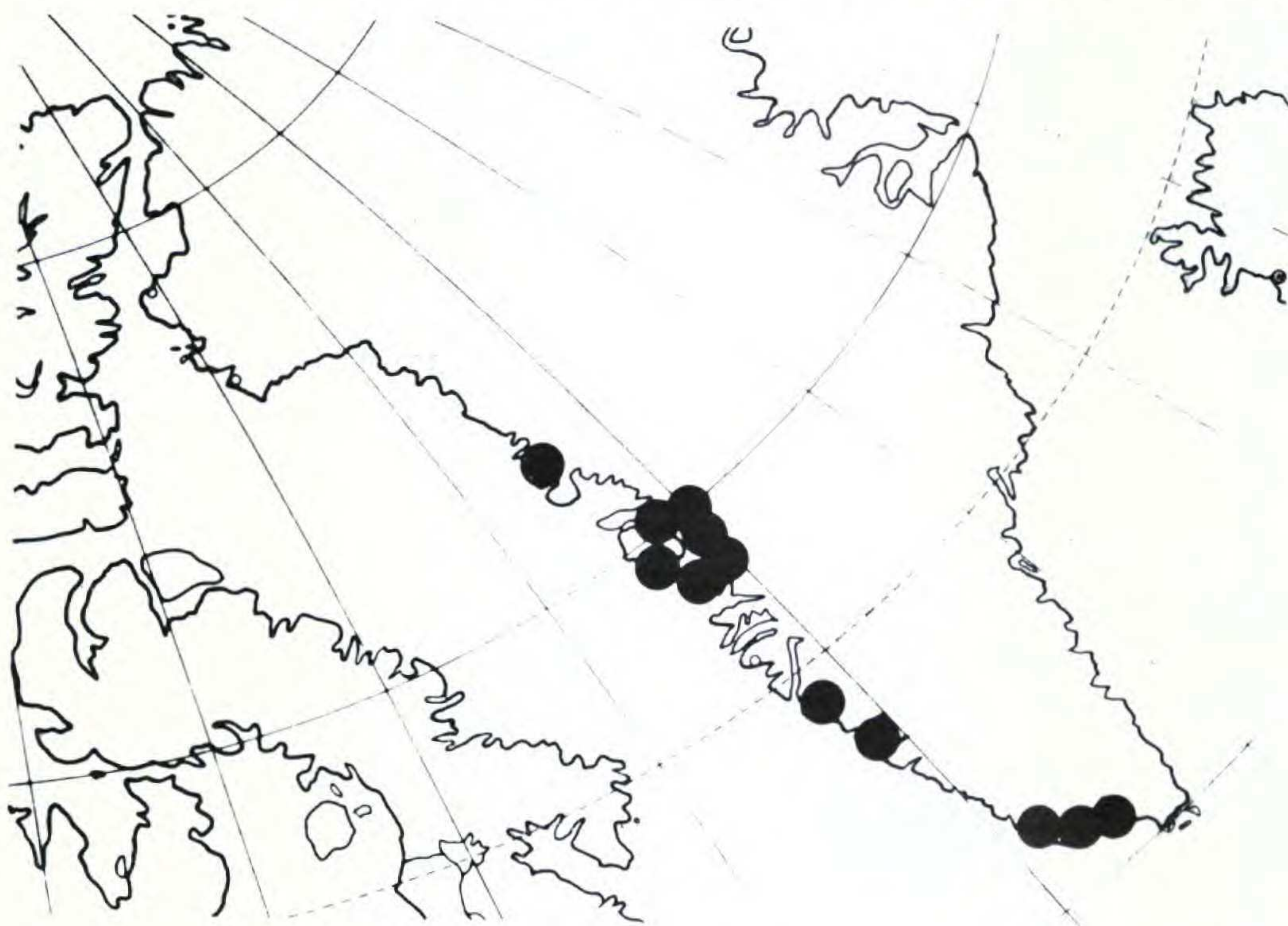


Fig. 14. Map of Greenland showing documented distribution of *Potamogeton groenlandicus*.

known only from non-fruiting material. However, both Fernald and Hagstrom overlooked the winter buds. In *P. groenlandicus*, the inner leaves of the winter buds are not modified into hardened fusiform structures, as in *P. pusillus*. Instead, the winter buds are similar to those of *P. obtusifolius*, in that the inner leaves are unmodified. To my knowledge, only one population of fertile individuals has been found, this being in flower. The flowers are most similar to *P. pusillus*. Because the winter buds and number of nerves are so different from *P. pusillus*, I am currently accepting *P. groenlandicus* at the specific level. However, material should be gathered and cultivated. If fruiting does occur, then the correct affinities of this endemic taxon can be ascertained.

REPRESENTATIVE SPECIMENS

GREENLAND: Christianshaab Dist.: Christianshaab, *Hartz* (C). Egedesminde Dist.: Egedesminde, 67°44'N, *Porsild* (CAN, GH, MO, NY, US). Frederikshaab Dist.: Frederikshaab, 62°00'N, 49°40'W, *Jørgensen & Larsson* (CAN); Ivigtut, *Berlin* (C). Godhavn Dist.: Disko, near Arktisk Station, 69°15'N, *Porsild* (CAN, F, GH, US); Disko, Godhavn, *Laegaard* 350 (CAN, US); Disko, near Godhavn, 69°14'N, *Porsild* 228 (GH, US); Disko, Sinigtik, 69°25'N, *Porsild* (CAN, GH); Disko, Skauseklippen, 69°25'N, *Porsild* (F). Godthaab Dist.: vicinity of Godthaab, 64°10'N, 51°43'W, *Porsild* 8273 (CAN); Godthaab Fjord, Itivnera, 64°22'N, *Porsild* (GH); Godthaab Fjord, Jersiutilik, *Trappnell* 402 (GH, K). Jakobshavn Dist.: Jakobshavn, *Sørensen* (C). Julianehaab Dist.: Igaliko Fjord, Qagssaarssuk, *Polunin* 10779 (CAN); vicinity of Julianehaab, 60°43'N, 46°05'W, *Porsild* 8120 (CAN). Ritenbenk Dist.: Ritenbenk, 69°44'N, *Hansen* (C); Sarkak, pool on gneiss, *Seward & Holttum* (CGE, K); 5 km E of Sarkak, *Beschel* 12163 (CAN, photo at DAO). Sukkertoppen Dist.: Ungarsivik Lake, 65°25'N, 52°50'W, *Porsild* 8870 (CAN). Upernavik Dist.: Laksefjord, Proven, *Porsild* 8837 (CAN).

ACKNOWLEDGMENTS

I am grateful to Dr. Ronald L. Stuckey, who supervised this study, for his advice and constant encouragement during the course of my work. Appreciation is also owed to Dr. Edward G. Voss for help with nomenclature; to Miss Judy Canne, Mr. Robert C. Gardner, and Mr. David Keil

for their helpful suggestions; to the curators of the herbaria from which specimens were borrowed; to the staffs at Kew Botanical Gardens and the British Museum for their painstaking search for the holotype of *Potamogeton strictifolius*; to the Linnean Society of London for the photograph of the holotype of *P. pusillus*; to my colleagues at the many libraries who supplied xerox copies of many original descriptions; to Mr. Robert C. Gardner, Dr. Pete Hostetter, and Mr. Robert Kalinsky for their help with the photographs; to Dr. Eugene C. Ogden, Mr. Stanley Smith, Dr. Edward G. Voss, and Dr. Steven Young for help in locating populations of *Potamogeton* in the field; and to Mr. Marvin L. Roberts, Dr. John A. Schmitt, and Dr. Tod F. Stuessy for their critical reading of the manuscript.

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DEPARTMENT OF BIOLOGICAL SCIENCES
LOUISIANA STATE UNIVERSITY IN SHREVEPORT
SHREVEPORT, LOUISIANA 71105